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PRESIDENTIAL ADDRESS

ON GERMINATING THE OOSPORES OF *PHYTOPHTHORA CACTORUM*

By ELIZABETH BLACKWELL, M.Sc., F.L.S.

Some spores germinate readily. One might say embarrassingly readily, thinking of the ubiquitous germlings from *Penicillium* conidia in the laboratory and from *Botrytis* conidia out of doors. For these it seems there is no obstacle to be overcome and there is no delay. The spores swell with imbibed water and the wall is stretched in one or more directions to give germ tubes. And this is so, even if some weeks of dormancy have been forced upon these air-borne spores by drought or a low temperature. The food reserves, and any growth-promoting substances there may be, are at once available; the wall at once permits the exit of a germ tube.

There are some spores which not only can but must germinate at once. Zoospores of water moulds as a rule germinate a few minutes after they are produced. The sporidia of plant rusts likewise must germinate at once or perish.

There are other spores which do not germinate readily: some not until months have elapsed, even years. They are called resting spores, and their common characteristic is that they needs must pass through a period of dormancy before germination. The exact nature of dormancy is not known; but dormancy of spores, like dormancy of seeds, is not a simple state. The early period of dormancy includes stages of maturation: e.g. deposition of reserves, wall formation, sometimes nuclear fusion; and while the spore is immature it does not, normally, germinate. The middle period includes changes in the protoplast and particularly in the reserves both within the protoplast and upon the inner face of the wall; perhaps changes in hydrogen-ion concentration affecting enzyme action and metabolism. The spore cannot germinate until this so-called 'after-ripening' is complete. The last period includes preparation for germination, e.g. assimilation of reserves, activation of growth-promoting substances, the breaking down of an impermeable wall, nuclear division; and the final step is the emission of the germ tube. These periods are of different lengths in different spores, and in any one spore they may be shortened or lengthened by external conditions during storage. The middle period, the period of 'after-ripening', is not always obvious. Some spores seem to pass steeply to the peak of maturation and then immediately begin the preparation for germination. For others there seems to be no 'peak' but rather a long plateau of after-ripening in the passage of which the spore, though mature, cannot proceed at once to germination. The teleutospores of *Puccinia malvacearum* and *P. graminis* differ not in the length of time they can remain dormant but in the length of time they must. The former will germinate almost at once: the latter not for some months except after special treatment. As Duggar once

expressed it: 'they need all the changes of the winter months.' It is this 'needs must' that is so surprising. Enforced dormancy one can, to a certain extent, understand. Whatever dormancy may be, it cannot be entirely suspended in these naturally dormant spores, but it can be shortened, and the various agents that have been used, as we say, 'to encourage germination', do shorten or 'break' dormancy one way or another.

Before proceeding to a review of these agents, and at the risk of stating the obvious, I would remind you that however much spores may be controlled in germination, they keep their own individual way of emitting a germ tube. In other words, they are genetically different, and this is dependent on the nuclear state which is beyond control of the agents about to be reviewed. This genetical difference is very strikingly brought home to one when observing uredospores and sporidia of *Coleosporium Tussilaginis* collected upon the same coverslip over an inverted van Tieghem cell. These golden spores, superficially not unlike, though the former is binucleate and the latter uninucleate, germinate in quite different ways: the former putting out two or three narrow germ tubes through germ pores, the latter swelling out into a single wide tube into which all the protoplasm at once passes. Another familiar example of the individuality of germinating spores is afforded by the conidia and ascospores of *Eurotium herbariorum*. The spiny conidia put out one or two germ tubes, while the ascospores form a germ tube as an expansion of the thinner belt which pushes aside the two lateral flanges. It is important to remember these genetical differences and to admit that there are limits to what one can do in controlling spore germination. No doubt there are limits too set by physiological differences of different spore types.

The agents that have been proved effective in germination of spores are those which have been used to break the dormancy of seeds, viz. a raising or lowering of the temperature, alternation of high and low temperatures, alternation of drying and wetting, light, 'nutrient solutions', 'volatile substances', the presence of the host of a parasite, some one common volatile substance generated by the presence of other living organisms in the same medium, carbon dioxide, bacteria, alkalinity, acidity, change of hydrogen-ion concentration, ionic content of the solution, and last but not least time.

A consideration of these various 'agents that encourage germination' leads one to suspect that the action is sometimes mechanical, sometimes chemical: that it may be upon the impermeable wall, upon the reserves or directly upon the living protoplast. For instance, a raising or lowering of temperature may initiate chemical changes in the reserves, or may have an indirect effect in producing by-products of decomposition which are themselves the activating agents. Alternating heat and cold and alternating drying and wetting may, like the process of weathering of rocks, cause minute cracks in a hard outer coat. A slight change of hydrogen-ion concentration may affect the composition of both wall and reserves, rendering for example the hydrophilic colloids more ready to imbibe water. And what can 'time' do? May it not be that in the slow metabolism of the living protoplast, enough carbon dioxide has accumulated to

change the hydrogen-ion concentration so that the colloidal state of reserves and wall is changed from within and the wall is made permeable to water and oxygen? Indeed, there comes a time when prompt germination must be the response to right conditions of air and water and temperature, and if these are not forthcoming the spore at last dies: its wall permeable and its reserves exhausted. There is, presumably, a limit to the viability of spores, although some may live for years, and it is a source of everlasting wonder how a microscopic spore can remain viable so long. Constant change must be taking place, else it would not be alive. But what incredibly slow metabolism this is.

At the risk of 'stating the obvious' once again I would remind you of the oft-demonstrated fact that for successful germination spores, as well as seeds, require water and air at a suitable temperature. A spore that has matured and completed its dormancy in water responds to aeration; an air-borne spore, ripe for germination, responds to moisture. These are the well-known 'conditions of germination', and remain the conditions of germination after the application of any of these various 'agents' that have been shown effective in *initiating* germination. But how low the oxygen supply may be I realized when germinating the resting sporangia of *Blastocladia Pringsheimii* in stale water under a coverslip sealed with wax to the slide (Blackwell, 1940), and how low the water supply may be has recently been pointed out by Brodie and Neufeld (1942) on germinating the conidia of *Erysiphe polygoni* at a humidity approaching zero.

The oospores of species of *Phytophthora* are peculiarly resistant to germination. de Bary (1881) reported germination of oospores of *P. omnivora* in 1866 and again in 1879. He kept the oospores for months in water and waited patiently for germlings, and he made the observation that oospores collected in June germinated more readily in the spring of the following year after a cold December. In 1914 Pethybridge found occasional germinating oospores of *P. erythroseptica* in cultures nine months old, and published satisfactory drawings by Lafferty of two of these. Lafferty and Pethybridge reported germination of oospores of *P. Syringae* in 1922. Rosenbaum (1915, 1917) made a serious attempt to germinate oospores of *P. Cactorum*, and after many failures in 1912 and 1913 with oospores of all ages, he tried burying the oospores out of doors over the winter of 1913–14, so that they should be, as he said, 'under as natural conditions as possible'. In 1917 he claimed that 'to date *Phytophthora Cactorum*... and *Phytophthora Fagi*... have been germinated... after a period of rest and under proper conditions'. Since that time to the present day there have been some half-dozen records of the finding of germinating oospores, usually in old cultures of these and other species of *Phytophthora*, but as Tucker (1931) writes in his monograph of *Phytophthora*: 'Definite observations on germinating oospores are few.'

Dormant oospores of this strain of *P. Cactorum* are colourless and transparent and perfectly spherical and lie loosely within the colourless oogonial wall, for at the height of their dormant state they have their minimum volume. The homogeneous protoplasm is enclosed within the double wall:

a thin transparent outer oospore wall and a thick transparent inner oospore wall. Within the protoplast are two striking objects: an excentric refringent globule which turns brown in osmic acid and is probably of highly saturated fat, and a small and yet more highly refringent body which turns black in osmic acid. It contains the nucleus and perhaps a plastid. One learns not to expect immediate germination in such a hard, shining oospore. In cultures which are several months old there may still be found oospores like this. There are others in which the protoplasm can no longer be discerned and the whole spore appears 'glassy'. These are dead. And yet again there are others which look active and vigorous, which are larger (almost filling the oogonial cavity), thin walled, the protoplasm more abundant and with the appearance of a uniform emulsion in which lie several refringent globules among which the nucleus is not readily distinguished. These are preparing for germination.

There is no doubt that the precise conditions that ensure germination of the oospore lie within narrow limits. A drop of water is all that is required to germinate an oospore which has been formed under proper conditions, which has been stored in a slowly drying medium, which has been allowed to lie dormant for the right length of time (which time is partly determined by the temperature at which the oospore has been kept), and finally whose three protective envelopes have been at last rendered permeable by various physical and chemical means. It is not to be wondered at that the drop of water does not cause immediate germination of all the oospores it moistens in a culture of fully matured and after-ripened oospores, which are enlarged until they fill the oogonial cavity and press against the oogonial wall, whose reserves are already assimilated into the cytoplasm, whose nuclei have undergone three or four divisions, whose walls are thin; oospores which, in fact, appear to be just on the point of germination. In such a culture of oospores as a rule only a few at a time will be found germinating.

Many unsuccessful attempts were made, in the early years of this study, to germinate in quantity the oospores of *P. Cactorum*. At first the experiments were of a desultory nature: of the 'hit or miss' variety, anything and everything previously found effective in spore germination being tried in the hope that by chance a successful method might be found. And in the end it was by chance that a way was found. It was in December 1924 that a few oospores were seen to be germinating *in situ* in two nine-month-old cultures on slopes of potato-mush agar which had been inoculated in the previous March and were still moist, a condition due in part to the large size of the test-tube in use and the considerable depth of agar. It is just possible that a drop of water of condensation may have initiated the germination (the culture had been kept on the laboratory bench subject to the fluctuating temperature of day and night) but fresh water it seems is not necessary: the moist, stale medium is enough. One of these nine-month-old cultures contained bacteria and percentage germination was, if anything, higher in this tube. In nature, bacteria must abound in the rotting tissues of the host and in the soil where the oospores presumably germinate in due course. Experiments were made later with cultures

which had been especially inoculated with bacteria and these were found to compare favourably with pure cultures in the quantity of germinating oospores.

At this stage of the investigation then, the special conditions that seemed necessary for germination of these oospores were: (*a*) a certain minimum age for full maturation of the oospore (it appeared to be nine months); (*b*) a slowly drying medium, never quite dry. It seemed too that bacteria were helpful in some way.

In February 1929 a culture only four months old (inoculated 18 October 1928) was examined and found to be full of oospores in a particularly vigorous state, apparently on the point of germination. To a portion of this culture, water was added (6 February 1929), and on the following day a few oospores were found with germ tubes. Clearly neither a great age nor the presence of bacteria (for this culture was clean) were necessary factors in germination. Inquiry showed that on 15 January the culture had been taken from an incubator (20° C.) and sent by hand, exposed on the journey to a temperature little above freezing-point, and afterwards kept on the laboratory bench (15° C.). It seemed that chilling of the oospores might be a means of obtaining germination. Acting on this hypothesis some preliminary experiments were made with chilling. Some cultures were kept out of doors on a flat roof leading from the laboratory, and controls were kept both on the laboratory bench at about 60° F. (= 15° C.) and in the incubator at 23° C. The results of this trial were encouraging enough to proceed with definite experiments on refrigeration as a means of encouraging germination, and these began in 1932.

Cultures were made in groups of three (A, B and C) in flasks or tubes, with a fair depth of agar; and they were inoculated at any time of year but usually in March, July and November. All three cultures of any one group were kept for the first month on the laboratory bench (15° C. approx.). Then culture A was put out on the roof shaded from direct sunlight and exposed to a wide range of day and night temperature. A maximum and minimum thermometer hanging beside the culture recorded the extremes of temperature. Culture B was stored in the refrigerator room attached to the college kitchen where the temperature varies around 35° F.: it may fall to freezing-point, or rise to 45° F. and over, when much in use and the door frequently opened. Culture C was kept, as a control, on the laboratory bench. But it was an unsteady control for two reasons: (*a*) the laboratory temperature, 60° F. during the day, dropped at night and on Sundays, when the heat was turned off, to 45° F.; (*b*) cultures kept in the laboratory dried up sooner or later and the oospores died of drought. The cultures A, B and C were frequently tested for germination and compared. A fresh piece of mycelium with oospores was taken each time and soaked in water, the main body of the culture being returned immediately to the special conditions under which it was kept.

After three years of experimenting thus, it was quite clear that refrigeration could be used as a practical method of encouraging germination. The C cultures that remained moist long enough gave germination after eight or nine months, but rarely in any quantity. The A cultures gave

erratic results, usually poor, but sometimes in winter very good, and then it was found that low temperatures had been recorded out of doors. Observations on the A cultures were complicated by the heavy production of chlamydospores on hyphae which grew during spells of milder weather. The B cultures did not develop conidia or chlamydospores, or indeed grow much at all; but their oospores steadily and quickly ripened at a temperature just above freezing-point and, when three months old, gave ready germination.

In 1939 a fresh impetus was given to the work when Miss Waterhouse joined me and with meticulous care repeated these experiments and explored further. Two lines of inquiry were followed. Firstly, was there any other set of conditions, or any other substance, which would either successfully replace chilling as a means of obtaining abundant germination of oospores, or intensify the results so far obtained, and how far were other agents limiting factors? Secondly, could germination of oospores younger than three months be obtained by chilling and subsequent soaking in tap water, and if so what proportion of time should be allowed (*a*) for ripening of the oospores, (*b*) for chilling, (*c*) for soaking in water? The following trials were made with unchilled oospores to see if other means could be found of breaking dormancy; and again with chilled oospores to see if the effects of chilling could be intensified.

Enzyme extracts were used to try to digest away the impermeable walls or at least to render them more permeable. Potato-skin extracts were made for the sake of the tyrosinase known to be present, because tyrosine had, from microchemical tests, been suspected in the inner oospore wall. Different strengths were tried for different lengths of time. The effect was to raise the percentage germination of chilled oospores, but germination was rarely abundant and then not more than 50 %. Spores which germinated in the extract soon had their germ tubes digested away if not removed to distilled water.

Yeast, known to contain a variety of enzymes and growth-promoting substances, was tried. The effect of the yeast extract, however, was to retard germination. The cultures treated showed vigorous hyphal growth, with sporangia, from the old mycelium. It appeared that the growth-promoting substance was affecting the mycelium but not its oospores.

The proprietary horticultural product Hortomone A was tried, and the effect was strikingly parallel to the action of the yeast extract. It is possible that growth-promoting substances cannot penetrate the outer oospore wall.

McKay (1937, 1939) had obtained a high percentage of germination with oospores of *Peronospora Schleideniana*, using potassium permanganate. His method was followed, but the oospores treated gave about the same percentage germination as the controls.

Since volatile substances, including carbon dioxide, have been found effective in spore germination, and as this suggested the production of acid conditions which might affect the spore walls, weak acids were tried. (This had at least the secondary value of destroying other parts of the fungus, viz. hyphae and less protected spores, and so rendering observation

on the resistant spores less obscure.) Spores dipped in 3 % sulphuric acid for less than a second are not killed but germination is inhibited or retarded.

And as it seemed that the helpful effect of bacteria might possibly be to render the medium alkaline (Berridge, 1924) weak alkalis, ammonia (*p*H 8·2), lime water (*p*H 8·0–10·0), baryta water (*p*H 8·0–10·0) and alkaline tap water (*p*H 7·6–8·0) were tried, both alone and alternately with weak acids. Considering the colloidal nature of the oospore wall, it seemed likely that slight changes of hydrogen-ion concentration might affect the water absorption of the hydrophilic colloids, especially changes from slightly acid to slightly alkaline conditions. In all the alkaline media percentage germination was higher than in distilled water (which was slightly acid *p*H 6·6). Lime water gave good results but no better than tap water. The tap water in use was, however, found to be slightly alkaline (*p*H 7·6–8·0) and to have a comparatively high calcium content (estimated at 19 parts in 100,000). It was then suspected that increased germination was due not so much to the presence of hydroxyl ions as to certain other ions, notably calcium. Further experiments on alkalis were therefore worked in conjunction with those concerned with the calcium content in relation to the hydrogen-ion concentration.

The outcome of these and other experiments made by Miss Waterhouse was to confirm the previous finding that the usual procedure of chilling the oospores and then soaking them in refreshed tap water cannot be bettered (provided the tap water has approximately *p*H 7·6–8·0 and Ca 15–19).

Miss Waterhouse then proceeded to experiment with the time factor, and by orderly and precise means she shortened the requisite time to two months, with a minimum of one week's refrigeration when the oospores are about a month old.

Change of condition may be an important factor in the actual germination (i.e. exit of germ tube): e.g. (*a*) alternate drying and wetting, causing cracking, (*b*) alternate heating and chilling, causing cracking (and this change may be between almost zero and laboratory temperature or between laboratory temperature and hot water), (*c*) alternate alkalinity and acidity, changing the colloidal state (and this may explain the observed fact that water refreshed at intervals is better than either continuous standing water or running water).

No exact specifications can be made about the age of spore that can most usefully be treated, the ideal period of treatment or the time required for soaking in water before the germ tube is put out; but it is possible to a certain extent to give instructions for successful germination of the oospores of *P. Cactorum*, thus: given well-formed and normal oospores (1) allow full maturation (at least one month) at 10–15° C. under moist conditions (neither wet nor completely dry); (2) allow a further period of dormancy under similar conditions (one to eight months); (3) refrigerate at a temperature just above freezing-point for a week or two; (4) soak in water (the following have been proved satisfactory: tap water of *p*H 8·0 and Ca content 19; soil solution of *p*H 7·0 and Ca content 15); (5) change the

solution daily or at least at frequent intervals; (6) wait for one to three (or more) weeks for germination.

When interpreting the results of germination it must be remembered that each oospore is an individual unit. It has been specially formed with its own nuclear fusion, its own thickness of wall, its own amount of reserves; it has its own size, its own age. There is no 'mass production' of oospores. And so all will not germinate at once. There may be one or two on the first day, and more on succeeding days until all viable ones have germinated. The non-viable ones may be immature, or they may be dead, having been stored under too hot or too dry conditions (dead oospores are easily recognized by a hard glassy look which is unmistakable), or they may have entered upon a state of 'secondary dormancy'. This condition is not understood, but it is a deeper dormancy than the first. The oospore looks just primed for germination, but the magic touch is rare and elusive that will break down the last barrier. This seems to lie in the relation of the outer oospore wall to the activity of the protoplast within.

As one would expect, these oospores are stored under perfect conditions in nature when they are in the ground over winter, and the warmth and rain in spring gives perfect conditions for germination. But that the oospores are as variable and as resistant in nature as in the laboratory is probable, and herein lies the success of the parasite. No set of conditions, however favourable they appear to us to be, are optimum conditions for all these spores. There is enough variety in the size and age of the spore, in the nature and thickness of the different walls, and in the nature and amount of the reserves, quite apart from difference of treatment, to prevent wholesale germination.

But the question still remains: what exactly is the dormancy of these oospores of *P. Cactorum* and how can refrigeration affect it? To attempt to answer this question it is necessary to know the composition of the enveloping wall layers and the nature of the reserves. Two sources of information are: (1) their microchemical reactions at different stages of development, and (2) the history of their development.

From unpublished work done by Miss Waterhouse on the microchemistry of the substances of the spores, I may pass on, with her kind permission, this information:

The oogonial wall has traces of fatty acids and at least three other constituents:

(*a*) A substance which is removed by treatment with chlorine water and sodium sulphite. This may be a hemicellulose.

(*b*) Cellulose which gives characteristic reactions after the hemicellulose has been removed and which can be dissolved away by cuprammonia.

(*c*) Something which remains as a resistant framework after both (*a*) and (*b*) have been removed.

There is reason to believe that the oogonial wall is not impermeable to water, but owing to its inelasticity it may offer mechanical resistance to the swelling of the spore within.

The outer oospore wall is characteristically inert: it gives few reactions:

(*a*) Insolubility after prolonged treatment with 72 % sulphuric acid.

(*b*) A great extensibility when treated with concentrated sulphuric acid, and other strong acids.

(*c*) A yellow or brown colour with iodine reagents.

(*d*) A red colour with ruthenium red.

This wall and the protoplasm are all that remain after treatment with 72 % sulphuric acid, revealing the protoplasmic origin of the outer oospore wall direct from the oosphere membrane and the periplasm. It is of complex protein and pectic material and is the most resistant and most impermeable layer.

The inner oospore wall gives reactions which suggest that the wall is of a triple nature having a basis of cellulose impregnated with some hemicellulose and a tyrosine compound. Later a substance appears that gives a bright blue colour with lacmoid. This may be callose though it does not give all reactions for callose. Whereas the outer oospore wall is highly *extensible*, the inner oospore *swells* enormously in sulphuric acid. This is a layer mainly of reserve food material.

The other source of information as to the nature of these wall layers and the reserves is a close observation of their formation during maturation of the oospore and their fate on germination.

The oogonial wall originates from the hyphal wall. After the oogonia and antheridia are cut off by septa from the hyphae which have borne them, their walls undergo some change, and not exactly the same change in each as is readily shown by the different colour they give with chlor-zinc-iodine. They are both extraordinarily resistant to bacterial action and to strong chemicals. On germination of the oospore the antheridium is as a rule still attached to the oogonium and the oogonial wall has to be forcibly cracked by the swelling oospore. This is so difficult sometimes that a germ tube may be seen winding about within the oogonial wall unable to make a way out. The firm and persistent nature of this wall must often inhibit germination.

The outer oospore wall begins as a plasma membrane, i.e. it is protoplasmic in origin. It is formed at a very early stage, beginning as the oosphere membrane before fertilization. After fertilization it becomes rapidly firmer and upon it is deposited the thin nucleated periplasm whose degenerating nuclei stain readily at this stage with nuclear dyes. It becomes impermeable and is undoubtedly the layer most difficult of penetration by water and gases, and the seat of greatest resistance to germination. It is finally extended by pressure of the swelling protoplast within but restricted by the oogonial wall without.

The inner oospore wall is deposited from within upon the outer oospore wall. It is formed very rapidly within a day after fertilization, and long before nuclear fusion. But it is not absorbed as rapidly as it is formed, and on preparation for germination its compound nature can be seen. While it is being slowly digested by the protoplast it has an eroded appearance: radiating lanes can be seen in it, which suggest that along certain radii are the more easily digested substances. This process is dependent on internal

activity of the protoplast and independent of entry of water. Quite often the germ tube grows out before this layer is completely absorbed, and this half-digested inner oospore wall may be left behind in the otherwise emptied oospore. This depends apparently on how soon the outer oospore wall permits water to enter.

It appears then that dormancy in these oospores may be attributed to several causes, and here are some of them:

(1) *Incomplete maturation.* The antheridial and oosphere nuclei do not fuse at once on entry of the former into the latter. The delay may be as long as a month, and although the inner oospore wall and the fat globule appear to be fully developed, the spore is not ripe until nuclear fusion has taken place.

(2) *Incomplete dormancy.* No germination has been obtained under two months. Digestion of the deposit of cellulose and protein which we call the inner oospore wall, and desaturation and assimilation of the oil globule do not begin until after nuclear fusion and take at least a month. In fact these reserves are often not completely assimilated if germination takes place so soon.

(3) *Mechanical resistance of the oogonial wall.*

(4) *Impermeability of the outer oospore wall.*

These causes of dormancy are strongly reminiscent of dormancy in seeds, and earlier this year the Fellows of the Linnean Society discussed 'Time, temperature and humidity in the germination of seeds'. Although one is a multicellular organ and the other usually not more than a single cell, seeds and spores have much in common (I am again stating the obvious). They each have an impermeable envelope: the seed has a cuticle, the spore has an epispore. Each may have a weak spot in this envelope; in the seed it may be the micropyle or the hilum, in the spore the point of entry of the fertilization tube or the point of abstriction. Their constitution is alike in that they both have substances in wall and reserves in a colloidal state, on which hydrophilic colloids depends in part the intake of water. Investigators of both seeds and spores have pointed out that the germination is in part controlled by the conditions under which development took place and by conditions of storage. Both seeds and spores may pass into a state of secondary dormancy, if preparation for germination has begun and been interrupted.

The use of chilling as a means of breaking dormancy is well known for seeds as well as spores. From the Boyce Thompson Institute (Barton, 1939) has recently come a recommendation for the after-ripening of certain seeds, viz. storage in moist condition at a temperature of 33–49° F. for two, three or more months. What can be happening at these low temperatures? We are told that in the freezing of a gel the configuration of colloidal systems is altered, because, on freezing, a gel ice separates, leaving relatively dehydrated gel and, on thawing, all the water is not at once or indeed readily reabsorbed. And again we are told of the metabolism of fats and oils and of the production of auxins at low temperatures. Chilling, then, may act mechanically in producing minute cracks in the impermeable

wall layers, or chemically by encouraging reactions that proceed best at a temperature just above freezing point.

I have said enough to indicate the high complexity of this spore and the difficulty of defining the exact conditions of its germination. We are concerned here with elaborate chemical substances: proteins, pectins, hemicellulose, cellulose and fats and these in colloidal state. The problem must be passed on to the biochemist and biophysicist and the student of cell-wall structure who some day may enable us to answer the questions that as yet remain unanswered: What are the precise conditions under which water is at last permitted to enter the spore and the germ tube to grow out? and how does chilling help?

Meanwhile the oospores continue to germinate one at a time and never all together, but with some remaining over for another time.

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Note

Pending the publication of the papers cited below, (1) tables of the results of experiments in germination of the oospores and (2) tables of microchemical reactions, together with coloured diagrams of these, are available for reference at Royal Holloway College and may be consulted there.

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FURTHER OBSERVATIONS ON AQUATIC HYPHOMYCETES OF DECAYING LEAVES

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(With Plates V and VI and 6 Text-figures)

Introduction

Recently an account was given (Ingold, 1942) of a flora of aquatic Hyphomycetes on submerged decaying leaves of alder from a stream in Leicestershire. This stream, which drains Cropston Reservoir, flows between fields and its banks are lined mainly by alders with occasional willows, and leaves of these trees make up the main mass of organic debris in the stream-bed.

From January to April 1942 samples of oak leaves were examined from the tiny streams which flow through Swithland Wood. These streams are from one mile to a mile and a half from the Cropston stream and are not connected with it, but, like it, they finally reach Swithland Reservoir. In spring, the beds of the streams in Swithland Wood are lined with decaying oak leaves. When samples of these were brought into the laboratory and kept at 15–18° C. for a day in large dishes of shallow water, rich crops of aquatic Hyphomycetes developed. Of the sixteen species already reported on alder leaves, the following thirteen occurred on the oak leaves, most of them in abundance and with great regularity, especially if the leaves had decayed almost to leaf-skeletons: *Tetracladium Marchalianum* De Wild., *Clavariopsis aquatica* De Wild., *Lemonniera aquatica* De Wild., *Varicosporium Elodeae* Kegel., *Tetrachaetum elegans* Ingold, *Alatospora acuminata* Ingold, *Articulospora tetracladia* Ingold, *Heliscus longibrachiatus* Ingold, *H. aquaticus* Ingold, *Anguillospora longissima* (Sacc. & Syd.) Ingold, *Tricladium splendens* Ingold, *T. angulatum* Ingold and *Flagellospora curvula* Ingold.

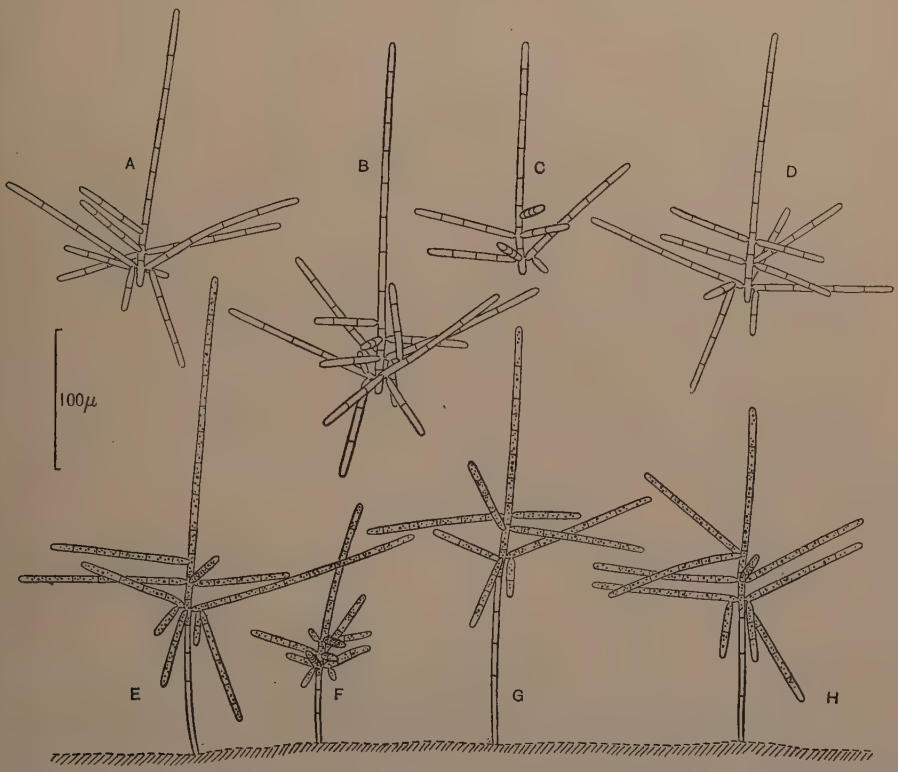
With these thirteen species two other submerged aquatic Hyphomycetes were common on the oak leaves. From the end of January to the middle of April some ten collections of decaying oak leaves were made, at roughly weekly intervals, from Swithland Wood, each of from ten to twenty leaves either in the leaf-skeleton condition or approaching that state. The two new fungi described below were found on some leaves of every collection.

Dendrospora erecta n.gen., n.sp.

The branched septate vegetative hyphae of this fungus ramify within the veins of the decaying oak leaves, and the conidiophores project at right angles into the water (Text-fig. 1 and Pl. V). In most aquatic Hyphomycetes miniature forests of conidiophores grow out from the decaying oak leaves, and hundreds, or even thousands, may be seen on a single leaf, but in *Dendrospora* the conidiophores may occur singly or, more usually, in

groups of rarely more than a dozen. This species seems to produce a few large spores rather than many smaller ones. I have rarely seen more than twenty or thirty conidiophores on a single leaf.

The conidiophore is straight, 50–120μ long, 4μ broad and 2–4-septate. A single branched, septate conidium of the aleuriospore type is formed terminally. The conidium (Text-fig. 1 and Pl. V, figs. 4, 6 and 7) consists of a long main axis with lateral branches, some of which branch again.



Text-fig. 1. *Dendrospora erecta* n.gen., n.sp. A–D, spores; no cell-contents are shown. E–H, conidiophores; the dots represent the oil-drops in the cells of the spore, but no other cell-contents are shown. In F the spore is still young and neither the main axis nor the branches have nearly reached their final length. The tissue of the oak leaf is indicated diagrammatically.

All the text-figures in this paper were drawn with the aid of a camera lucida, from living specimens.

The main axis of the spore is straight, of uniform width, and continuous with the conidiophore. It is 150–300μ long, 4–5μ broad, 8–12-septate with each cell containing a number of small oil-drops. From the lower region of this main axis, but rarely more than 50μ from its base, branches arise usually in pairs or in whorls of three, the number of such whorls or pairs varying from two to four. These primary laterals grow out at right angles to the main axis. They are 2–8-septate, 50–180μ long, 4–5μ broad and each is abruptly constricted to about 2μ where it joins the axis. The

lowermost of these branches may branch again to give secondary laterals which always arise near the bases of the primary ones. These secondary laterals are 10–90μ long, 4–5μ broad and, like the primary ones, are constricted to 2μ at their bases.

Since the conidiophore passes without change of width or direction into the main axis of the spore, it is not clear, at first sight, where the conidiophore ends and the conidium begins. The actual junction is at the cross-wall immediately below the insertion of the lowermost branches of the spore. This was indicated by an examination of liberated spores and by watching specimens in hanging-drop cultures when disjunction at this cross-wall was observed. Thus the specimen shown in Pl. V, fig. 2, was kept under observation for a number of hours and the spore was seen to separate at the point shown by the arrow. One feature distinguishes the cells of the spore from those of the conidiophore; all the cells of the spore contain several small oil-drops, but in the cells of the conidiophore these are absent or poorly developed.

The degree of branching of the spore varies considerably, the number of primary laterals being six to twelve and secondary laterals one to five. The largest spores are remarkably big, being more than a third of a millimetre long and quite bushy, they can be seen with a hand lens of low power.

In water the spores germinate very slowly or not at all, but they germinate readily in 2 % malt solution, or on malt agar, by means of rather narrow germ tubes which develop from the ends of the main axis and from the tips of the branches.

On malt agar a branched, septate, hyaline mycelium is produced, but, although I have grown this organism in unifungal culture, I failed to secure colonies free from bacteria.

This fungus is especially interesting when compared with the aquatic Hyphomycetes previously described (Ingold, 1942), because the branched spore appears to reach the highest development yet observed. When compared with the other aquatic Hyphomycetes with branched spores, it seems to bear the greatest resemblance to *Tricladium splendens*. In both fungi the conidium is a terminal aleuriospore produced singly at the end of a conidiophore normally unbranched. In both the main axis of the spore is continuous with the conidiophore and laterals are produced which are constricted abruptly at their junction with the axis. However, in *T. splendens* there are only two lateral branches and these, in contrast to the six to twelve of the present species, do not give rise to secondary branches.

In spite of the resemblances it seems clear that this fungus cannot be placed in the genus *Tricladium*, and because of the tree-like form of the spore the generic name *Dendrospora* is proposed.

Dendrospora n.gen.

Submerged aquatic fungi with branched, septate mycelium. Conidia (aleuriospores) terminal, septate, branched, each consisting of one main axis with several secondary and tertiary ramuli.

Dendrospora gen.nov.

Fungi aquatici submersi mycelio repente, septato, ramoso. Conidia (aleuriosporae) acrogena, septata, ramosa, ex uno ramo principali et ramulis secundariis et tertiariis compluribus constantia.

Dendrospora erecta n.sp.

Submerged aquatic fungus with branched, septate, hyaline mycelium. Conidiophores simple, 50–120μ long, 4μ broad, 2–4-septate. Conidia (aleuriospores) apical, hyaline, septate, branched; main axis 150–300μ long, 4–5μ broad, continuous with the conidiophore; secondary ramuli 6–12, 50–180μ long, 4–5μ broad, constricted at the base to 2μ, arising (usually in pairs or in whorls of three) from the lower part of the main axis; tertiary ramuli, which may arise from the lowermost secondary ramuli, 10–90μ long, 4–5μ broad, constricted at the base to 2μ.

On submerged decaying leaves of *Quercus* sp. from streams in Leicestershire, England.

Dendrospora erecta sp.nov.

Fungus aquaticus submersus, mycelio repente, hyalino, septato, ramoso. Conidiophora simplicia, 50–120μ longa, 4μ lata, 2–4 septata. Conidia (aleuriosporae) acrogena, hyalina, septata, ramosa; ramus principalis 150–300μ longus, 4–5μ latus, cum conidiophoro continuus; ramuli secundarii 6–12, 50–180μ longi, 4–5μ lati, basi ad 2μ constricti, plerumque bini vel verticillato terni, ex inferiore parte rami principalis orientes; ramuli tertiarii ex infimis ramulis secundariis aliquando exorientes, 10–90μ longi, 4–5μ lati, basi ad 2μ constricti.

Hab.: in foliis putrescentibus *Quercus* sp. in fluminibus jacentibus Leicestershire, Anglia.

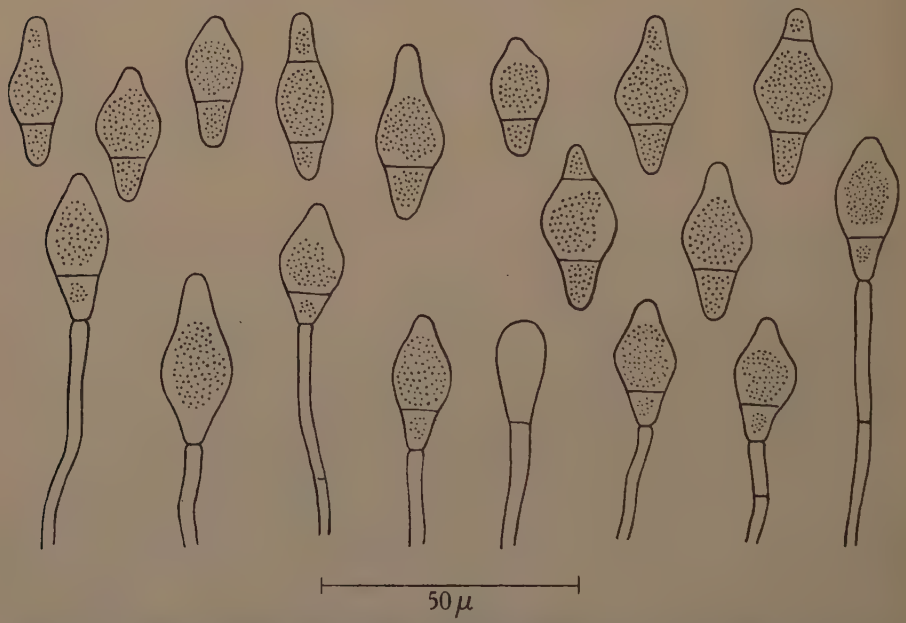
Piricularia aquatica n.sp.

This fungus (Text-figs. 2–5 and Pl. VI, figs. 1–6) was common on submerged decaying leaf-skeletons of oak in the streams of Swithland Wood in Leicestershire from January to April 1942. It was also seen on similar leaves collected in April from a stream near Westerham, Kent, and once on a submerged decaying leaf of hawthorn from the stream which drains Cropston Reservoir in Leicestershire.

The mycelium of the fungus appears to be within the veins of the leaf with the conidiophores projecting at right angles into the water. The conidiophore is usually 20–60μ long, 2–3μ broad and bears a single terminal conidium of the aleuriospore type. The conidia, formed below water in nature, are somewhat lemon-shaped, 24–34μ long, 12–16μ broad, hyaline and usually two-celled with the upper cell much larger than the lower. The conidia are often three-celled and then the middle cell is large with a small one above and below it. Occasionally the spores are unicellular. The conidia have a pearly appearance due to an abundant supply of glycogen.

The fungus was isolated in single-spore pure culture on malt agar. On this medium a very compact colony of branched septate hyphae was formed.

The hyphae were colourless at first, but soon became grey with a slight greenish tinge. The mycelium was mainly on the surface of the agar or slightly submerged, although there was also a very sparse growth of greyish green aerial hyphae reaching a height of seldom more than 1 mm. Many of these hyphae had terminal or intercalary hyphal coils. The general colour of the colony was greenish grey, but the central zone was greyish yellow, due to a brilliant orange-yellow pigment, produced in the medium by the older parts of the mycelium, in combination with the grey of the hyphae. In a colony thirty-two days old, grown on malt agar at 16–18° C. and having a diameter of 6·6 cm., the central zone (3·5 cm. in diameter)



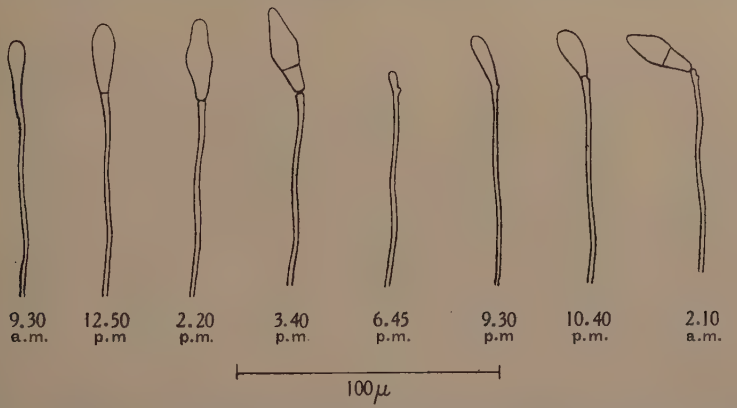
Text-fig. 2. *Piricularia aquatica* n.sp. Spores and conidiophores. The only contents shown are the glycogen vacuoles which are indicated by stippling. In one spore attached to a conidiophore (fifth from the left) development has not proceeded far and no glycogen has yet accumulated. From decaying oak leaves.

was dominated by the yellow pigment; outside this was another zone (1·4 cm. wide) of pale greenish grey, and finally a very narrow zone (0·15 cm. wide) of uncoloured hyphae forming a white fringe. Cultures grown in the dark showed no zonation, but those grown in ordinary light were sharply zoned by concentric rings of daily growth.

Using spores from the decaying leaves, a large number of single-spore cultures were made. For the first week or so none of these produced any aerial spores, but when a strip of a colony was immersed in water very abundant conidia were produced on submerged conidiophores within twenty-four hours. These agreed with the submerged aquatic conidiophores observed in nature, but the spores tended to be rather longer and narrower

(Pl. VI, figs. 1, 2). At the moment of liberation these spores were usually 1-septate, but there was a strong tendency for an additional septum to form, delimiting a small apical cell, before germination occurred. Like those found on the leaves, the spores were hyaline and contained abundant glycogen.

Development of the spores was watched in hanging-drop pure cultures and the course of this is shown in Text-fig. 3. The first spore to be produced is truly terminal and, when ripe, it separates from the conidiophore. Then, just to one side of the cross-wall which originally separated the conidiophore from the first spore, a protuberance is produced from the end of the conidiophore which is soon cut off as the primordium of the second spore. This type of successive conidium (aleuriospore) development from the apex of the conidiophore is reminiscent of *Trichothecium roseum* and is also similar to what occurs (Ingold, 1942) in *Articulospora tetracladia* and *Tricladium angulatum*.



Text-fig. 3. *Piricularia aquatica*. Spore development as seen in hanging-drop pure culture. The first spore, arising in a truly terminal position, was liberated about 4 p.m.; the succeeding spore about ten hours later.

When first isolated some of the single-spore cultures, after ten days or so, produced aerial conidia rather sparingly on short conidiophores (Text-fig. 4) which arose as lateral branches of certain aerial hyphae. The aerial conidia are clearly homologous with the submerged aquatic conidia, but there are certain striking differences. First, the aerial conidia (Text-fig. 5) are mostly greenish brown, due to pigmentation of the cell walls, although they are sometimes hyaline. Secondly, they are normally three-celled with the middle cell much the biggest, whilst the submerged aquatic spores tend to be two-celled. Thirdly, in the cells of the spore are numerous oil-drops in contrast to the glycogen of the aquatic spores.

Although at first aerial conidia were produced sparingly on certain of the single-spore cultures, others failed to form such spores. Further, after two months in culture on malt agar, subculturing on to the same medium invariably gave colonies which, although they grew with apparently undiminished vigour, failed to form aerial spores.

The aquatic spore germinates readily in 2 % malt solution or on malt agar by a germ tube produced from each pole of the spore.

The classification of this fungus is difficult, especially in view of the differences in the aleuriospores produced below water in nature and aerially

Text-fig. 4. *Piricularia aquatica.* Undisturbed aerial conidiophores growing in pure culture on malt agar. The shading on the spores is to show their form; it does not represent their contents. Under the conditions of illumination used, the interior of the spores and hyphae could not be distinguished and cross-walls, which may have been present, were not visible.

in pure culture on malt agar. As the fuscous, 2-septate, aerial spore passes through a hyaline and 1-septate stage during its development, it might be argued that it is the 'higher' type and that it is this spore which should determine primarily the genus of the fungus. On the other hand, the hyaline aquatic spores are the only ones known, so far, in nature.

I owe to Mr E. W. Mason the suggestion that, if this fungus is to be included in an existing genus, it might well find a place in *Piricularia*. The 2-septate conidia in that genus may be hyaline or fuscous. They are borne on simple erect aerial conidiophores and the production of conidia in succession resembles that in *Trichothecium roseum*. Indeed, the type species, *Piricularia grisea* (Cooke) Sacc. was originally described as *Trichothecium griseum* Cooke. There are, however, difficulties in associating the present species with *Piricularia*. Species of that genus are mostly parasites of grasses; the spore of all the described species shows a minute abscission collar, and the greatest width of the spore is near to its base and not near the middle as in my fungus.

Text-fig. 5. *Piricularia aquatica.* Aerial conidia from pure culture on malt agar. The oil-drops in the cells are shown. Fuscous cells are shaded.

Accepting Mr Mason's tentative suggestion, I am placing the fungus as a new species of *Piricularia*, although with further knowledge of aquatic Hyphomycetes, its systematic standing may have to be reconsidered.

Piricularia aquatica n.sp.

Submerged aquatic fungus with branched, septate mycelium, hyaline at first, dark olive green later. Submerged aquatic conidiophores 20–60μ long, 2–3μ broad. Aquatic conidia (aleuriospores) hyaline, lemon-shaped, 24–34μ long, 12–16μ broad, usually 1-septate near the base, rarely unequally 2-septate with the middle cell largest, containing abundant glycogen; first-formed conidium truly apical, subsequent conidia produced in succession from near the same point. Aerial conidia (aleuriospores) produced sparingly on malt agar. Aerial conidiophores straight, 40–50μ long, 2–3μ broad. Aerial conidia narrowly lemon-shaped, 24–42μ long, 8–12μ broad, greenish brown (rarely hyaline), usually 2-septate with the middle cell largest, containing numerous oil-drops; first-formed conidium truly apical, subsequent conidia produced in succession from near the same point.

On decaying leaves of *Quercus* sp. from a stream in Leicestershire, England.

Piricularia aquatica sp.nov.

Fungus aquaticus submersus, mycelio repente, ramoso, septato, primo hyalino postea olivaceo-fuscescente. Conidiophora aquatica submersa 20–60μ longa, 2–3μ lata. Conidia aquatica (aleuriosporae) hyalina, citriformia, 24–34μ longa, 12–16μ lata, plerumque prope basim 1-septata, raro inaequaliter 2-septatum, cellula media majore, abundanter glycogeno. Conidium primo evolutum apicale; conidia succedentia prope eundem locum deinceps evoluta. Conidia aeria (aleuriosporae) parce in agaro ('malt agar') evoluta. Conidiophora aeria recta, 40–50μ longa, 2–3μ lata. Conidia aeria citriformia, 24–42μ longa, 8–12μ lata, glaucobrunnea (raro hyalina), 2-septata (media cellula majore), multis guttulis oleosis praedita; conidium primo evolutum vero apicale, conidia succedentia prope eundem locum deinceps evoluta.

Hab.: in foliis putrescentibus *Quercus* sp. in fluminibus jacentibus Leicestershire, Anglia.

Tricladium anomalum n.sp.

This fungus (Text-fig. 6 and Pl. VI, figs. 8–10) was found growing on submerged decaying leaves of reedmace (*Typha latifolia*) in a large pond known as Puddledyke situated close to Cropston Reservoir. It was observed in three separate collections made during April 1942 and again in quantity at the end of May and in August. The only other aquatic hyphomycete noted on the leaves of reedmace was *Alatospora acuminata*.

The branched septate mycelium ramifies within the tissues of the decaying leaf and the conidiophores grow out at right angles into the water. The conidiophore is simple, 50–100μ long, 3·5–4·5μ broad and 2–3-septate. The conidium, which is of the aleuriospore type, is septate and branched, consisting of a main axis (continuous with the conidiophore) 150–250μ long, 3·5–5μ broad, and of usually three lateral branches. At the point where a lateral branch arises the main axis tends to be bent to

an obtuse angle. Each lateral is 80–120μ long, 4–5μ broad where it joins the axis, but tapers to 2–3μ at its free end. The branches usually lie in different planes. Of the very numerous spores observed, more than three-quarters were five-pronged, consisting of a main axis and three laterals, but a number were four-pronged with only two branches, and some six-pronged spores, consisting of a main axis and four laterals, were observed.

A number of single-spore pure cultures were made on malt agar. The fungus grew well on this medium, giving a mycelium of branched septate hyphae. These were hyaline at first, but soon turned brownish grey, so

Text-fig. 6. *Tricladium anomalum* n.sp. Conidia and conidiophores. In the four conidiophores figured, the junction of the conidium and the conidiophore is probably the second cross-wall below the lowest branch of the spore. No cell contents are shown. The tissue of the reedmace leaf is indicated diagrammatically.

that a colony two to three weeks old was dark brownish grey with a narrow white edging of hyaline hyphae (Pl. VI, fig. 7). There was much low aerial growth of brownish grey hyphae, giving the whole colony a fleecy appearance. This fungus did not sporulate on agar or on strips of colony immersed in water.

The fungus strongly resembles *Tricladium angulatum*. In both species, the conidium consists of a main axis, with broadly inserted laterals tapering to their extremities, usually bent to an obtuse angle at the point of origin of each lateral. There are striking differences, namely: (1) in *Tricladium anomalum* the axis of the spore normally bears three lateral branches instead

of two; (2) the spores of *T. anomalum* are much larger than those of *T. angulatum*; (3) each conidiophore is simple and appears to produce only one spore, whereas in *T. angulatum* the conidiophore is usually branched, and when unbranched the first formed conidium is truly terminal with later spores produced in succession from near the same point; (4) the culture on malt agar is brownish grey in contrast to the white colonies of *T. angulatum*; and (5) a strip of colony fails to sporulate in water, but a similar strip of *T. angulatum* produces abundant spores in water.

I have no doubt that this species is quite distinct from *T. angulatum*, but it is regarded as co-generic with that species in spite of the additional arm on the spore.

Tricladium anomalum n.sp.

Submerged aquatic fungus with branched, septate mycelium, hyaline at first but dark later. Conidiophores simple, erect, 50–100μ long, 3·5–4·5μ broad. Conidia (aleuriospores) apical, branched, septate, hyaline; main axis 150–250μ long, 3·5–5μ broad; branches usually three (rarely two or four), arising separately with intervals of 20–30μ, 80–120μ long, 4–5μ broad at the base and not constricted, tapering to 2–3μ at the apex; main axis usually curved or bent to an obtuse angle at the point of origin of each branch.

On submerged decaying leaves of *Typha latifolia* from a large pond in Leicestershire, England.

Tricladium anomalum sp.nov.

Fungus aquaticus submersus, mycelio repente, septato, ramoso, primo hyalino, postea fuscescente. Conidiophora simplicia, erecta, 50–100μ longa, 3·5–4·5μ lata. Conidia (aleuriosporae) acrogena, ramosa, septata, hyalina; ramus principalis 150–250μ longus, 3·5–5μ latus; ramuli secundarii plerumque tres (raro duo vel quatuor), separatim orientes, intervallis 20–30μ, 80–120μ longi, basi 4–5μ non constricti, apice ad 2–3μ attenuati; ramus principalis plerumque curvulus vel iisdem locis e quibus ramuli secundarii oriuntur obtuse angulatus.

Hab.: in foliis putrescentibus *Typhae latifoliae* in lacu, Leicestershire, Anglia.

Distribution of aquatic Hyphomycetes

My observations on aquatic Hyphomycetes have been limited, so far, to the immediate neighbourhood of Cropston in Leicestershire, but it is of interest to know if they are of wide occurrence. Unfortunately it has not been possible to undertake a general investigation of their distribution. However, during April 1942, a collection of submerged decaying leaves of oak and sweet chestnut was made from a small stream near Westerham in Kent. These leaves yielded the following species: *Clavariopsis aquatica*, *Tetracladium Marchalianum*, *Piricularia aquatica*, *Tricladium splendens*, *T. angulatum*, *Anguillospora longissima*, *Lemonniera aquatica*, *Alatospora acuminata*, *Heliscus longibrachiatus* and *Tetrachaetum elegans*.

Again, in August 1942, a collection of submerged decaying leaves of hawthorn was made from a stream in Skeffington Wood in east Leicester-

shire about ten miles from Cropston. These leaves were brown, but had not become lacunate by decay. The following seven species occurred in abundance on all the leaves examined: *Lemonniera aquatica*, *Anguillospora longissima*, *Clavariopsis aquatica*, *Tetracladium Marchalianum*, *Alatospora acuminata*, *Tricladium angulatum* and *Flagellospora curvula*.

These isolated observations strongly suggest that these fungi are widely distributed. It would be surprising if further observations do not show that many of these Hyphomycetes are very common on the decaying submerged leaves of trees and shrubs.

Summary

Of the sixteen species of aquatic Hyphomycetes previously described from decaying alder leaves (Ingold, 1942), thirteen are now recorded on decaying submerged oak leaves. In addition two new species, *Dendrospora erecta* n.gen., n.sp. and *Piricularia aquatica* n.sp., are described. These are regular members of the aquatic oak-leaf flora of the streams in Swithland Wood during the spring.

Tricladium anomalum n.sp. is described growing on decaying submerged leaves of *Typha latifolia* from a pond.

The distribution of aquatic Hyphomycetes is briefly discussed, and it is suggested that they are probably very common on submerged decaying leaves of trees and shrubs.

My best thanks are due to Miss E. M. Wakefield for her kindness in helping me with the Latin diagnoses.

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EXPLANATION OF PLATES V AND VI

Note. All the photographs are from living unstained specimens with the exception of Pl. VI, fig. 4.

Plate V. *Dendrospora erecta* n.gen., n.sp.

Fig. 1. Conidiophore with young developing spore. The cross-wall separating the conidium and the conidiophore is indicated by the arrow. × 280.

Fig. 2. A single mesh in the vein network of an oak-leaf skeleton showing a conidiophore. Without further growth the conidium separated from the conidiophore at the point shown by the arrow. × 92.

Fig. 3. Conidiophore bearing a ripe spore. Where the main axis of the spore joins the conidiophore is indicated approximately by the arrow, but the actual junction is obscured by the branches of the spore. Note the lateral branch produced by the conidiophore. No other branched conidiophore has been observed. × 140.

Fig. 4. Spore. × 137.

Fig. 5. Conidiophore with young developing spore in which the main axis and the branches have probably not reached half their final length. The arrow shows the junction of the conidiophore and spore. × 300.

Figs. 6, 7. Photograph and camera lucida drawing of the same spore. The photograph was taken after making the drawing and when the spore had been flattened into a single plane by pressure of the cover-glass. Corresponding branches in the two figures have been given the same numbers. The primary branches are indicated by Roman figures (I–VIII), and the secondary ones by ordinary figures. Thus 3*a* and 3*b* are branches of III. × 185.

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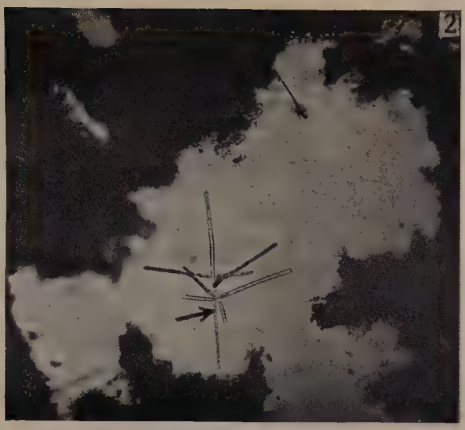
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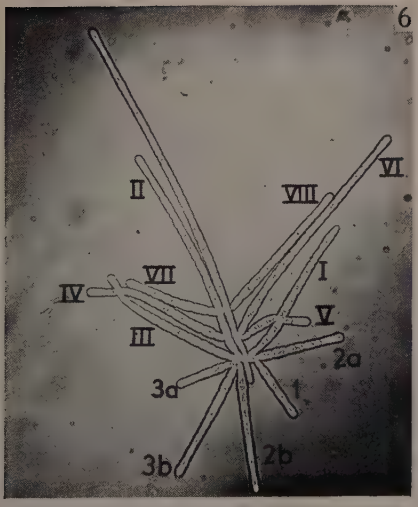
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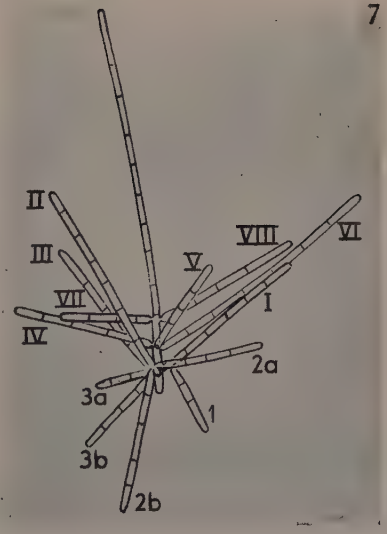
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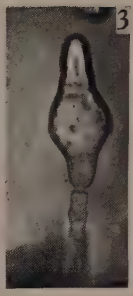
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PLATE VI

Figs. 1, 2. *Piricularia aquatica* n.sp. Aquatic conidiophores, with ripe conidia, developed from strips of pure culture submerged in water. × 532.

Figs. 3–6. *Piricularia aquatica*. Aquatic conidiophores, with ripe conidia, developed on submerged decaying oak leaves. The specimen shown in Fig. 4 was stained with iodine which gives a deep chestnut brown (black in the photograph) with the glycogen of the spore. Figs. 3 and 5, × 545; Fig. 4, × 490; and Fig. 6, × 525.

Fig. 7. *Tricladium anomalum* n.sp. Pure culture three weeks old grown on malt agar at 16–18° C. Natural size, photographed with reflected light.

Fig. 8. *Tricladium anomalum*. Conidiophore with developing conidium. The arrow shows the junction of the conidiophore and the conidium. '*T*' is part of the decaying reedmace leaf; '*B*' is a filament of the alga *Bulbochaete* sp. growing epiphytically on the reedmace leaf. × 200.

Fig. 9. *Tricladium anomalum*. Conidiophore with a nearly ripe conidium growing on a decaying leaf of reedmace (marked '*T*'). The arrow shows the junction of the conidium and its conidiophore. × 185.

Fig. 10. *Tricladium anomalum*. Conidium. × 185.

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A DISEASE OF LILIES CAUSED BY *FUSARIUM BULBIGENUM* COOKE & MASS.

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I. Introduction

In the summer of 1939 serious losses occurred among seedling lilies of various varieties at a nursery where lilies are grown in large quantities. Bare patches developed in boxes of one-year-old plants, and the plants bordering these patches had yellow, stunted foliage. Isolations from diseased plants invariably yielded a species of *Fusarium*.

No record has been found of a similar disease of seedling lilies, but species of *Fusarium* have been reported in association with diseases of mature plants. Thus *Fusarium Solani* (Mart.) App. & Wollenw. was isolated by van Hell (1931) from diseased roots and bulbs of lilies in Holland, but inoculation experiments gave negative results and he attributed the disease to *Cylindrocarpon radicicola* Wollenw. A root-rot of lilies caused by *Fusarium* was reported from America by Charles and Martin (1928) and by Slate (1936). More recently, Imle (1940) described a basal rot of bulbs of *Lilium candidum* and *L. testaceum* imported into the U.S.A. He isolated *Fusarium* from brown, rotted areas at the bases of the bulb scales.

II. Disease symptoms

Seedlings of *Lilium auratum*, *L. Sargentiae*, *L. nobilissimum* and a hybrid lily from the edges of bare patches in the seed boxes were obtained from the nursery. The first sign of infection was a slight wilting of the leaves. Wilted seedlings had rooted well and had formed small sound bulbs, but the roots showed a reddish brown rot which usually began at the tips. Seedlings in which the disease was more advanced bore yellow, stunted foliage. The roots were entirely rotted and the rot was spreading from the roots into the bulb scales. The junction between diseased and healthy tissue was clearly defined, the lower portions of the scales being completely rotted while the upper parts were white and sound. Hence infected scales readily became detached from the bulbs. The outer scales were attacked first. Some bulbs were wholly rotten. If diseased tissues were kept in a moist atmosphere a white mycelium bearing spores of *Fusarium* developed.

Reddish brown lesions occurred on the bulb scales, roots and the underground parts of the main stems of mature plants of *Lilium regale*, grown at the Imperial College Biological Field Station at Slough, and on bulbs of a hybrid lily stored at the nursery.

III. Isolation and identification of pathogen

Fusarium was obtained from each of 125 isolations made from diseased roots and bulbs of seedlings of various species, from bulbs, roots and stems of mature plants of *Lilium regale*, and from bulbs of a hybrid lily. A few bulbs also gave species of *Phytophthora*, *Penicillium*, *Rhizoctonia*, and *Trichoderma*.

All the isolates of *Fusarium* were morphologically similar, and a detailed study was made of a strongly pathogenic one from a damped-off seedling of *Lilium auratum*.

(*a*) *General cultural features*

Aerial mycelium typically well developed; loose cottony; colour varying from white to pink thus:

Potato agar: usually lacking.
Cornmeal agar, Oatmeal agar, Malt agar } pink to bluish pink.
Cornmeal agar + 1·5 % dextrose: deep blood-red.

Sclerotia noted on potato agar, oatmeal agar, Brown's medium and potato plugs; white or buff when young sometimes bluish later; diameter 1–3 mm.; generally distributed, but in old dried-up cultures particularly abundant along the line of contact of medium with culture tube; occasionally in cluster of 2–4 mm. diam.

Sporodochia abundant on oatmeal and potato plugs three weeks after inoculation; size 0·5–2·0 mm. diam.; slimy, buff coloured, becoming darker when older; sometimes formed in clusters of two or three.

In an old culture sectoring had taken place. The saltant produced very little mycelium and sometimes no aerial growth, and was less pathogenic than fresh isolations.

Optimum temperature for growth was approximately 30° C.

(*b*) *Microscopic features*

Microconidia, more abundant than macroconidia both in culture and on bulb; formed abundantly in aerial mycelium and in medium in false heads (*Cephalosporium*); 0–1 septate, oval or slightly curved, apedicellate.

Dimensions: 0-septate 2·8–18·5 × 2·5–3·7 μ, av. 7·4 × 3·1 μ;

one-septate 10·2–27·8 × 2·5–3·7 μ, av. 14·9 × 3·1 μ.

Macroconidia formed sparingly in mycelium in small pionnotes on potato and malt-agar media or in sporodochia on oatmeal agar; mostly three-septate, pedicellate, curved, terminal cell curved and somewhat constricted, tendency to degeneration in form; in young sporodochia (i.e. up to 0·5 mm. diam.) 90–95 % of macroconidia three-septate, remainder

four- to five-septate; in older sporodochia number of three-septate spores decreased to 80 %, remaining 20 % four- to five-septate.

Dimensions: three-septate 22·2–42·6 × 2·8–4·6 μ, av. 36 × 3·8 μ;
four-septate 33·3–44·4 × 2·8–4·6 μ, av. 38·7 × 3·8 μ;
five-septate 37–48·2 × 2·8–4·6 μ, av. 44·1 × 4·1 μ.

Chlamydospores formed in abundance on potato and oatmeal agars both in medium and on aerial mycelium, singly or in chains, not found in the bulb; in old sporodochia chlamydospores formed from segments of macroconidia.

Dimensions: 7·4–14·8 × 5·6–12·9 μ, av. 9·4–8 μ.

The presence of terminal and intercalary chlamydospores and abundant microconidia and the shape of the macroconidia indicate that this species of *Fusarium* should be placed in the section *Elegans*.

A strain of *Fusarium bulbigenum* Cooke & Mass. isolated from a *Narcissus* bulb with basal rot, resembled the strain under consideration. The resemblance of the latter to *Fusarium bulbigenum* described in Wollenweber's monograph (1935) suggested that it was probably a strain of that species. Miss E. M. Wakefield has kindly confirmed this identification.

IV. Inoculation experiments

Inoculation experiments were made with the strain of *Fusarium* from *Lilium auratum*. *Fusarium bulbigenum* isolated from *Narcissus* was included for comparison. In one series of experiments, roots, bulb scales and whole bulbs of *Lilium regale* and seedlings of *L. Wilmottiae* were inoculated, either by wounding or by contact, with agar inocula. In a second series seeds were sown and bulbs planted in soil contaminated with the *Fusarium*.

(*a*) *Inoculation with agar inocula*

Healthy bulbs of *Lilium regale* and of *Narcissus* var. Golden Spur were washed with 95 % alcohol, soaked for ten minutes in a 0·1 % solution of mercuric chloride, and finally washed in sterile water. Scales cut from healthy bulbs of *Lilium regale* and of *Narcissus* and pieces cut from healthy roots of *Lilium regale* were similarly treated (with the exception that roots were soaked in mercuric chloride for three minutes) and the cut ends were sealed with paraffin wax. Seedlings of *L. Wilmottiae* were washed in several changes of sterile water. These were then inoculated by placing a small piece of an agar culture either on the unwounded surface or in a wound which was sealed with wax. Small pieces of sterile agar were always applied as controls. These controls all gave negative results and are not included in the table. The inoculated material was kept moist for two to three weeks, or longer with whole bulbs, in a heated greenhouse, or in an incubator at 20° C. The results are given in Table 1.

Heavy infection followed when either the strain of *Fusarium bulbigenum* from lily or that from *Narcissus* was introduced into wounds in the surface

of whole bulbs or of isolated bulb scales of either *Lilium regale* or *Narcissus* or seedling bulbs of *Lilium Wilmottiae*. No infection of unwounded bulb scales took place. Both fungi penetrated unwounded roots of *L. regale* and of seedlings of *L. Wilmottiae*. *Fusarium bulbigenum* from lily penetrated unwounded seedlings of *Lilium Wilmottiae* at the junction of root and bulb, probably entering through the roots. The strain from *Narcissus* did not attack such seedlings but the number of trials was small. This fungus was always less pathogenic to lilies than was the strain isolated from *Lilium auratum*, for rotting due to the former was much slower than that due to the lily strain. The strain from lilies was less pathogenic to *Narcissus* than was the strain from that host.

Table 1

Material inoculated	Method of inoculation	*F. bulbigenum* from lily: No. inoc.	*F. bulbigenum* from lily: No. infected	*F. bulbigenum* from *Narcissus*: No. inoc.	*F. bulbigenum* from *Narcissus*: No. infected
L. regale, bulbs	Wound	60	55	44	40
	Contact	14	0	7	0
Narcissus, bulbs	Wound	61	41	21	21
	Contact	14	0	7	0
L. regale, bulb scales	Wound	29	27	18	18
	Contact	9	0	7	0
Narcissus, bulb scales	Wound	32	29	16	16
	Contact	14	0	7	0
L. regale, roots	Wound	8	8	5	5
	Contact	6	6	3	3
L. Wilmottiae, seedling, bulbs	Wound	20	20	4	4
	Contact	16	0	8	0
L. Wilmottiae, seedling, roots	Wound	16	16	4	4
	Contact	24	21	12	8
L. Wilmottiae, seedling, junction of roots and scales	Wound	8	8	4	4
	Contact	8	5	4	0

Table 2

Variety of lily	Soil	No. of seeds sown	Condition 6 months after sowing: No. healthy plants	No. slightly attacked *Fusarium*	No. severely attacked *Fusarium*
L. Wilmottiae	Autoclaved	40	27	1	0
	Infected*	40	8	3	5
L. dauricum	Autoclaved	40	30	1	3
	Infected*	40	6	6	6
L. Davidii	Autoclaved	40	21	0	0
	Infected*	40	8	3	6

* 3 parts autoclaved soil + 1 part soil from bare patch in seed box.

(*b*) *Soil inoculation*

(i) *Addition of naturally infected soil*

Soil from around diseased seedlings in seed boxes at the nursery was sifted to remove plant debris, mixed with three volumes of autoclaved soil and sown with lily seeds. The results of one such experiment are set out in Table 2 and show that the fungus was present in the soil. Other ex-

periments in which the soil inoculum was added to autoclaved soil or to unsterilized compost gave comparable results.

(ii) *Addition of fungal cultures to the soil*

Experiments were carried out in which seeds of *Lilium Wilmottiae*, *L. dauricum* and *L. Davidii* were sown in soil which had been inoculated with *Fusarium bulbigenum* isolated from lily seedlings or from *Narcissus* bulbs.

The fungi were grown for fourteen days at 20° C. on a mixture of sand and cornmeal (sand, 95 g.; cornmeal, 5 g.; water, 20 c.c.) in sterile plugged flasks. The cultures were then added to autoclaved potting compost at the rate of 2·5 g. to every 100 g. of soil. A similar quantity of sterile sand was added to autoclaved compost for control. Fifteen or occasionally ten seeds were sown in each 4 in. pot. Each experiment was replicated

Table 3

Strain of *F. bulbigenum* added to autoclaved soil	No. of seeds sown	No. germinated	No. subsequently damped-off	Percentage survivors
None	150	149	0	99·3
Fresh isolation, lily	150	114	72	28
Old isolation, lily	150	136	31	70
Fresh isolation, *Narcissus*	150	138	19	79·4

Table 4

Variety of lily	Strain of *F. bulbigenum* added to autoclaved soil	No. seeds sown	No. germinated	No. damped-off	% healthy plants of seeds sown
L. Wilmottiae	None	690	446	5	63·5
	Fresh isolation, lily	270	78	64	5·2
	Old isolation, lily	450	197	76	27·0
	Fresh isolation, *Narcissus*	150	95	18	51·3
L. dauricum	None	640	500	3	77·7
	Fresh isolation, lily	595	206	131	12·6
	Old isolation, lily	400	278	77	50·3
L. Davidii	None	565	420	13	72·1
	Fresh isolation, lily	595	131	112	3·4
	Old isolation, lily	300	149	54	31·7
	Fresh isolation, *Narcissus*	185	162	36	68·1
	Isolation from mature bulb, *L. regale*	150	64	6	38·7

ten times. The experiments were made in a heated greenhouse during the period September–April and in an unheated frame during the summer. The duration of individual experiments varied from ten to twenty-four weeks. The results of an experiment with seeds of *Lilium dauricum* are shown in Table 3 which gives the number of survivors eleven weeks after inoculation.

Additional experiments, which are summarized in Table 4, give essentially similar results. In a number of these the addition of a fresh isolate to the soil caused a much higher proportion of pre-emergence damping-off than in the experiment of Table 3. This may have been because the soil was kept rather wet in some of the earlier experiments. In all the experiments, however, the number of survivors in the presence of a recently isolated culture was small. Virulence decreased in culture.

In a single experiment with seeds of *Lilium Davidii* a strain from a mature bulb of *L. regale* caused losses equivalent to those due to an old isolation from seedlings. *Fusarium bulbigenum* recently isolated from *Narcissus* bulbs was also pathogenic but to a smaller degree than the strain from lily.

In three experiments, mature bulbs of *Lilium regale* were planted in the open over sand to which a sand and cornmeal culture of *Fusarium bulbigenum* from lily had been added. Control bulbs were planted over clean sand. In each experiment the shoots produced by the inoculated plants were slightly shorter and less vigorous than those from the controls. When the bulbs were lifted in autumn the roots of the inoculated ones were rotten at the tips while the outer bulb scales showed reddish brown lesions. *F. bulbigenum* was isolated from these. Rotting did not progress during storage and the bulbs were planted in clean soil after removal of the infected scales. The plants produced were healthy but smaller than those from the control bulbs. The presence of similar lesions yielding *F. bulbigenum* on mature bulbs of *Lilium regale* grown at Slough and of a hybrid lily grown at a nursery shows that slight infection of mature bulbs does occur under natural conditions. While the fungus does not kill the mature plant it is clear that a significant loss of vigour follows attack.

(iii) *Watering with spore suspensions*

Losses at the nursery where the disease was first observed took place chiefly among one-year-old seedlings. The seeds were sown in steam-sterilized soil, which was stored for several months after sterilization, during which time it might have become reinfected. It was unlikely, however, that there was an initial concentration of the fungus in the seed boxes comparable with that in the experiments described above. These seed boxes were watered from storage tanks underneath the benches, and this may have been the source of contamination. One would expect some time to elapse before much infection of the soil would develop from this source.

Six boxes of autoclaved soil were each sown with 125 seeds of *L. Wilmottiae*. Three of these were sprayed with a suspension of spores of *Fusarium bulbigenum* immediately after sowing and again after five and eleven weeks. All the boxes were watered with tap water. Six months after sowing the seedlings were examined. The three control boxes contained 285 seedlings, one of which was diseased, while in the inoculated lots there were 213 seedlings, forty-nine of which were diseased (i.e. 75·7 % of the seeds sown in the control boxes and 43·7 % of those in the inoculated lots produced healthy seedlings). These results were confirmed by a number of small-scale experiments.

In another series of experiments, seeds were sown in autoclaved soil and the seedlings were pricked out into unsterilized compost or autoclaved soil when the second foliage leaf had just uncurled. These were later inoculated by watering with spore suspension. In one such experiment seedlings of *Lilium Wilmottiae*, *L. dauricum* or *L. Davidii* were planted in autoclaved soil in well-drained sterilized tins. Half of these were watered with tap water only. The results with the three varieties were similar and will be given

collectively. Of sixty-six control plants, sixty-two were healthy after four months (four having been eaten off by slugs) while only eighteen out of sixty-six were healthy in the inoculated lots, the rest being more or less severely attacked by *Fusarium*. The other experiments in this series all gave comparable results.

Thus it is obvious that contamination of the water supply can cause infection and produce much loss during the long period (up to twenty-one months) that the seedlings remain in the seed boxes. It is unlikely, however, that the amount of contamination would be as great as that in the experiments described above, and losses from this source should be controlled by periodic cleaning of the water tanks and by covering them to prevent contamination from the benches.

V. Control measures

In the opinion of the grower concerned, losses were highest in the houses which were kept at a relatively high temperature. This was confirmed by a small-scale experiment at Slough and is comparable to the behaviour of *Fusarium bulbigenum* on *Narcissus* which was shown to cause heavier losses at a relatively high temperature (Gregory, 1932; Hawker, 1935, 1940). Although losses were less at a low temperature they were not negligible, for severe loss occurred in cold frames. Moreover, any reduction in the temperature of the houses is undesirable because it retards the lilies. Attempts were therefore made to control the disease by means of fungicides.

(*a*) *Formalin dust in seed boxes*

Since possible sources of infection were incomplete sterilization or re-contamination of the soil used to fill seed boxes or frames, the effect of the addition of a fungicide to the soil was examined. As it was difficult to obtain large quantities of lily seed it was not possible to compare the effects of a wide range of fungicides. In a preliminary experiment, formalin dust was compared with an organic mercury fungicide. The former was greatly superior and was used in all subsequent experiments.

Three parts by volume of autoclaved soil were mixed with one part each of peat and sand. This was inoculated by adding a small quantity of naturally infected soil or of a sand and cornmeal culture of *Fusarium bulbigenum* (prepared as described in the previous section) and was stored for at least one month before the addition of the fungicide. In earlier experiments formalin dust was prepared after the formula of Alexander, Young and Kiger (1931) by adding fifteen parts by weight of commercial formalin (40 % formaldehyde) to eighty-five parts of 1:2 mixture of kaolin and diatomaceous earth. (This preparation had been used successfully by Tandon (1939) in the control of a damping-off disease of tomatoes.) In later experiments the method was simplified by using air-dried soil as absorbent. In all experiments 0·5 % by weight of the formalin dust was added to the inoculated compost. This was thoroughly mixed and put into pots or boxes which were sown two days later and stored either in a heated

greenhouse or in a cold frame. The results of a typical experiment are given in Table 5. Other experiments all gave comparable results.

Table 5

Variety used	Soil treatment	No. of seeds sown	Total germinated	No. diseased	% clean seedlings of seeds sown
L. Davidii	Compost*	120	96	0	80
	Compost* + *F. bulbigenum*	120	36	30	5
	Compost* + *F. bulbigenum* + formalin dust	120	97	19	65
L. Wilmottiae	Compost*	120	73	2	60·9
	Compost* + *F. bulbigenum*	120	11	8	2·5
	Compost* + *F. bulbigenum* + formalin dust	120	60	9	42·5

* Autoclaved soil + peat + sand.

Thus formalin dust gave good but not complete control. It is unlikely that the contamination of the seed boxes prepared by the methods in use at the nursery would be as heavy as that in the experimental boxes, and then the degree of control might well be adequate.

A small-scale experiment was also set up at the nursery. Five seed boxes were prepared in the usual manner by the nurseryman. Three were left untreated, while 0·5 % formalin dust was thoroughly mixed with the soil of the other two. All were sown with seeds of *Lilium auratum* a few days later (July 1939). The seeds germinated well in all boxes, but by the early summer of 1940 the treated ones showed a denser stand with larger leaves. In October 1940 the grower reported that 'the foliage on the two treated boxes was twice as large and plentiful as on the other boxes'. The foliage later died down naturally and the boxes were turned out early in 1941. It was not possible to obtain detailed results without interfering unduly with the grower's routine but some observations and counts were recorded. The bulbs from the two treated lots were much more numerous, bigger and better rooted than those from the untreated lots. The treated boxes were very similar, and one which was examined in detail contained 355 bulbs (one of which was slightly diseased) weighing 728 g. The roots of all the sound bulbs were white and healthy. The three untreated boxes were much less uniform. The worst and the best of these contained respectively fifty-eight bulbs (seven diseased) weighing only 77 g. and 102 bulbs (ten diseased) weighing 196 g. Hardly any of these had entirely unattacked roots, whilst the compost contained much rotten debris from badly diseased bulbs which had broken up owing to the destruction of the bases of the scales by the fungus. The grower pointed out that the treated boxes were overcrowded and would have probably yielded better results if they had been sown more thinly than was customary. This suggests that thin sowing on treated soil may lead to economy in the use of valuable seed. It seemed likely that infection at this nursery was usually due either to incomplete soil sterilization or to slight recontamination before sowing. The use of formalin dust promised to give good control there, but the

experiment could not be repeated the following year because the houses were required for food production.

(*b*) *Liquid formalin in frames*

Large quantities of lilies were raised from seed in cold frames at the nursery. Steam sterilization of the soil in these frames was less efficient than in seed boxes, and losses from *Fusarium* were heavy. The grower considered that the use of formalin dust on this scale would require too much labour. Therefore the efficacy of liquid formalin was tested. A small frame at the Field Station was contaminated with a sand and cornmeal culture of *Fusarium bulbigenum* and another was filled with compost brought from a frame at the nursery where the disease had been rampant. Half of the first frame was treated with commercial formalin (40 % formaldehyde) at the rate of 1 c.c. per 25 sq. cm. early in March and covered for several days. The frame was sown with seeds of *Lilium dauricum* one week later. The seeds in the treated half were a few days later in germinating than those in the control part, but by mid-June the former were green and healthy while the latter were dying as a result of attack by *Fusarium*. Later, the foliage of both lots was severely damaged by *Botrytis*. In the following March the bulbs were lifted. The treated half yielded fifty-six bulbs, eleven of which were slightly diseased while the control half yielded only fourteen bulbs all of which were more or less severely rotted. Half of the second frame was treated with formalin at twice the above rate (i.e. 2 c.c. per 25 sq. cm.) in July, and sown with seeds of *Lilium regale* one week later. By September the treated half showed a distinctly better stand than the untreated half. In the following March* eighty-five seedlings, three of which were slightly diseased, were lifted from the treated part while the control part yielded sixteen seedlings, six of which were diseased. Thus some protection was obtained by the use of liquid formalin in frames containing heavily contaminated soil, and it is possible that more satisfactory results could be obtained by the use of a greater quantity of formalin applied some time before sowing. Further experiments were prevented by war conditions.

(*c*) *Watering with fungicides*

Owing to the length of time that lily seedlings remain in the seed boxes or frames, severe losses may easily follow if the soil be accidentally re-contaminated. An attempt was made to prevent losses by watering with weak fungicidal solutions.

In one series of experiments seeds were sown or seedlings pricked out in autoclaved soil mixed with clean sand and peat. When the seedlings were established they were watered with a suspension of spores of *Fusarium bulbigenum*, or infected soil was sprinkled around them. After an interval of from two days to one month they were watered with a weak fungicidal

* Seedlings of *L. regale* are normally lifted in late autumn, but the frame used here was required for other purposes. It is unlikely that any of the control plants would have survived until November.

solution. Formalin was useless when used in this way, and a 0·02 % solution of the proprietary mercuric fungicide 'Uspulun' was used in most experiments. The results of two small-scale experiments in which some protection was obtained by six weekly applications of Uspulun are given in the first five lines of Table 6. Other small-scale experiments confirmed this result, but an experiment on a larger scale was spoiled by *Botrytis* before the boxes were turned out. Before this attack, however, the stand in the Uspulun-treated boxes was much denser than that in the controls.

Table 6

Source of infection	Treatment	No. of seeds or plants	No. clean plants	No. diseased plants
Infected soil	None	100 seeds	49	28
	6 weekly applications of 0·02 % Uspulun	100 seeds	70	6
None	None	66 plants	62	0
Spore suspension	None	66 plants	18	28
	6 weekly applications of 0·02 % Uspulun	66 plants	59	2
Infected soil	None	125 seeds	10	6
	2 applications of 0·02 % Uspulun (5 l. to 1500 sq. cm.)	125 seeds	36	0
	Treated formalin before planting	125 seeds	82	3
	Treated formalin before planting+2 applications of 0·02 % Uspulun	125 seeds	85	2

In the second of the two experiments described in the previous section half of the untreated and formalin-treated areas were watered with Uspulun after the seeds had germinated. Some protection was obtained (last four lines of Table 6), but this was not so good as with formalin treatment before sowing, while watering with Uspulun did not increase the efficacy of the formalin treatment.

A large-scale experiment was also made at the nursery. A range of fifteen cold frames showed a poor stand of one-year-old seedlings of *Lilium regale*. All the frames were well watered with tap water and six were then given 1 pint per sq. ft. of a 0·02 % solution of Uspulun. The disease was established before treatment, but when the seedlings were dug six months later the treated lots were slightly better. The bulbs were cleaned and divided by the grower into good and bad lots, the latter including both diseased and very small bulbs. These were counted and weighed. The average number of bulbs from the six treated frames was 286 (wt. 1223·8 g.), of which 235 (wt. 1027·5 g.) were classed as good while the average yield from the nine untreated frames was 204 bulbs (wt. 989·4 g.) of which 156 (wt. 745 g.) were classed as good.

Thus the use of formalin dust in the seed boxes gives good control of the disease, while the use of liquid formalin in the frames and occasional watering with a weak solution of Uspulun during the growing period offer further promising methods of control.

VI. Summary

A disease of seedling lilies was found to be due to *Fusarium bulbigenum* Cooke & Mass. Disease symptoms and the morphology of the pathogen are described in detail. A similar fungus was isolated from lesions on mature bulbs.

Inoculation experiments showed that the fungus can enter unwounded roots of *Lilium regale* and of seedling lilies but cannot penetrate unwounded bulb scales. A strain of *Fusarium bulbigenum* from *Narcissus* caused rotting of wounded bulb scales but rotting was slower than with the lily strain.

A high incidence of both pre-emergence and post-emergence damping-off of lily seedlings occurred in autoclaved soil contaminated by soil from the vicinity of diseased seedlings or by sand and cornmeal cultures of *Fusarium bulbigenum*. The strain from *Narcissus* caused less heavy losses. Old isolations of the lily strain were less virulent than fresh ones.

Watering the seed boxes with a suspension of spores of *Fusarium bulbigenum* caused losses.

The addition of a formalin dust to the seed boxes before sowing gave good control. Watering the soil in frames with liquid formalin before planting, or watering the growing seedlings with a weak solution of Uspulun gave some control.

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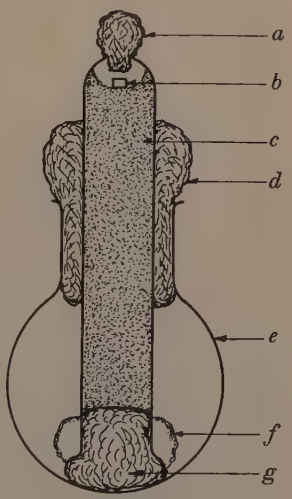
METHODS FOR OBTAINING FRUCTIFICATIONS OF WOOD-ROTTING FUNGI IN CULTURE

By E. C. BADCOCK, *Forest Products Research Laboratory, Department of Scientific and Industrial Research*

(With Plate VII and 1 Text-figure)

In 1941 I described a medium consisting of sawdust to which various nutrients were added, on which many wood-rotting fungi make exceptionally vigorous growth. The formation of fructifications was noted in eight of the twenty species listed. Since then, by using the methods described below, six more of the species there listed, together with sixty-seven additional species, have fruited on the sawdust medium. Many of these fungi have not previously fruited on other media in this laboratory.

It had been observed that in cultures of *Polystictus versicolor*, *Trametes serialis* and *Fomes pinicola* growing in large tubes almost completely filled with the sawdust, the mycelium would grow through the plugs and begin to form fructifications, if the tubes were kept in a metal-lined incubator in which a fairly high relative humidity was maintained. This suggested that it might be desirable to maintain around the mouth of the tube a relative humidity rather higher than is normally present in the laboratory. For the formation of normal fructifications, it is necessary in most species to expose the cultures to light for considerable periods, and this is not readily achieved in an incubator. Moreover, contamination of the plugs with moulds sometimes occurred in the incubators, so the following method was devised which keeps the plugs sterile and reproduces the humid conditions of the incubators.



Text-fig. 1.

Text-fig. 1 shows the general arrangement of the culture vessel. *c* is a boiling tube in which a small hole has been blown in the bottom—the tube is packed rather firmly with the sawdust medium and then plugged with cotton wool in the usual way, the small hole also being plugged: the tube is then placed with the open end in a wide-mouthed flask *e*, in which there is a pad of wet absorbent cotton wool. The space in the neck of the flask around the tube is filled with a cotton-wool plug *d*. The apparatus is then sterilized in an autoclave for 30 min. The transplant of fungus mycelium is introduced through the small hole and the small cotton-wool plug sealed down with a little plasticine to prevent drying out, and to prevent the fungus growing out at this end. The mycelium grows along the tube

through plug *G* and fructifications usually develop around the mouth of the tube within the flask. In this way the developing fructification is kept in a relatively moist, but not saturated, atmosphere without risk of contamination. This method is very satisfactory for producing fruit bodies of *Trametes serialis*.

Some fungi do not form mature fruit bodies in a confined space such as the flask described above, possibly owing to the absence of ultra-violet light or to too high a humidity. When a fungus produced an abortive fruit body, which ceased to develop further or formed a hymenium which was becoming overgrown with vegetative mycelium, either the tube, together with the plug *d*, was removed, or if the fruit body was attached to the damp wad *f*, the plug *d* was carefully unwound without disturbing the tube, which was then wedged into position. When the tube is removed it is supported on two Petri dish lids (see Pl. VII, fig. 2), the dish nearer the mouth being filled with water. A thick strip of absorbent cotton wool, saturated with water, was placed on the plug with its ends resting in the dish of water, and a pad of moist cotton wool was placed beneath the fruit body. This dish and pad were never allowed to dry out, since even temporary drying of the fruit body often prevents any further development. The cultures should not be exposed to direct sunlight for at least a couple of days after removal from a dark incubator, and certain fungi, such as *Polyporus Schweinitzii*, should never be exposed to direct sunlight even for a few minutes. Most fungi develop best in strong diffused light, and in this laboratory they are grown on shelves about 8 ft. from a large window, which is open on most days. The amount of ultra-violet light falling on the fungi was probably of the same order as that in moderate shade outdoors.

A more rapid method, which does, however, involve more risk of contamination, is to fill large tubes (30 × 8 cm. or 20 × 4 cm. have been used) with the sawdust medium so that the base of the cotton-wool plug comes well into contact with the medium. The mouth of the plug should be wiped free of sawdust before the plug is inserted. Because of the bulk of medium in the larger size of tubes it is advisable to autoclave them at 15 lb. pressure for 1 hr., half an hour being sufficient for the smaller size. The plugs should not project more than 2 cm. beyond the mouth of the tubes and should not fit tightly. In order to reduce the risk of contamination in the larger tubes inoculation of the medium is effected through a small glass tube in the large plug, and this itself has a small separate plug. The large plugs should not be flamed when carrying out inoculations, as the presence of charred cotton may check the growth of the mycelium through the plug. If paper labels are used the gum should contain an antiseptic to prevent moulds developing on them.

After inoculation the tubes should be kept in an incubator in which a moderately high humidity is maintained, by having a dish of water exposed in it. If the plugs are not sufficiently moist for the mycelium to grow freely through them they can be moistened occasionally with a few drops of water, for it is important that the growth of the fungus should not be checked by drying out. After the mycelium has reached the ends of the tubes they are removed from the incubator and placed in the light on

Petri dishes containing water as described above. Pl. VII, fig. 1, shows fruit bodies of *Pleurotus ostreatus* developed by this method.

The most rapid method of obtaining fruit bodies is to remove the plugs entirely when the mycelium has grown about half-way down the tube and then to place a wad of wet absorbent cotton wool in the mouth of the tube just out of contact with the medium; later, when vigorous surface growth is developing, this pad may be gently pushed down, so as to touch the medium. The tubes containing the pads are then placed on Petri dishes containing water, in such a position that the light from the window falls on the open mouths of the tubes. Pl. VII, figs. 3 and 4, shows fruits of *Ganoderma resinaceum* and of *Merulius tremellosus* respectively, developed in this way. The tubes may be tilted slightly so as to facilitate the addition of water to the absorbent pads. When the fruit bodies of agarics begin to develop the tubes are best stood up vertically in baskets and a little water added daily. If the atmosphere of the laboratory is very dry a ring of absorbent wool may be tied around the end of the tube and kept moist.

Certain agarics were found to develop fructifications more readily when the amount of accelerator in the sawdust was increased, and up to 40 % of the total was sometimes used. These fungi also require on the whole rather higher moisture contents, and the medium should initially contain about two and a half times its dry weight of moisture.

It was found that fleshy agarics that normally form long stipes, fruit best in tubes half-filled with the sawdust medium. This enables the pileus to form inside, or just outside, the rim where the atmosphere is relatively moist. When attempts are made to obtain fruits of an unidentified species, a tube half-filled with the sawdust medium is a useful supplement to the other cultures. (Pl. VII, fig. 5, shows a fruit body of *Pholiota adiposa* developed by this method.)

Although contamination with moulds is occasionally troublesome when the plugs are entirely removed, yet when the wood-destroying fungus is growing vigorously, fruit bodies are usually developed before any extensive mould growth becomes evident. Generally speaking, moulds develop on these sawdust cultures only when the fungus has ceased to grow actively.

In the table a list of the fungi tested is given, and it will be noted that in eighty-two out of the ninety-two species tested fructifications were formed. Of the ten species which did not fruit all but one were old isolations.

Conditions necessary for formation of fructification in laboratory

No single standard method can be expected to induce fructification in all species of wood-rotting fungi equally, for they behave very differently under natural conditions. Some form fruit bodies in a few months after the tree or log is infected; others, such as *Trametes Pini*, do not normally fructify until many years after the tree is infected. Some species form their fructifications throughout the year, others only during a limited season, and it is evident that they vary greatly in the amount of light which they require to produce typical sporophores. *Coniophora cerebella* and *Trametes*

List of fungi grown on sawdust medium

The fungi were isolated at the Forest Products Research Laboratory except where the name of the supplier is stated.

Fungus	Time between inoculation and fruiting (if any) weeks
Armillaria mellea (Vahl) Fr. (2 strains)	No fruiting
A. mucida (Schrad.) Fr.	6
Collybia velutipes (Curt.) Fr.	7
Coniophora cerebella Pers.	10
Daldinia concentrica (Bolt.) Ces. & de Not.	No fruiting
Echinodontium tinctorium E. & H. (Mounce, Canada)	8 (Ab.)
Flammula sapinea Fr.	No fruiting
Fomes annosus Fr. (2 strains)	8
F. Clelandii Lloyd (McClennan, Australia)	8½
F. conchatus (Pers.) Fr.	10
F. fomentarius (Linn.) Fr.	7
F. fraxineus (Bull.) Fr.	7½
F. igniarius (Linn.) Fr. (2 strains)	11–12
F. lividus Kalchbr. (Lurie, South Africa)	8½
F. melanoporus Mont. (Bagchee, India)	9
F. pinicola (Sw.) Cke.	10
Ganoderma applanatum (Pers.) Pat.	11
G. oregonense Murr. (Mounce, Canada)	No fruiting
G. resinaceum Boud.	12
Hydnum coralloides (Scop.) Fr.	7
H. erinaceus (Bull.) Fr.	6
Hypholoma sublateritium Schaeff.	31
Irpex obliquus (Schrad.) Fr.	6½
Lentinus cochleatus (Pers.) Fr.	7
L. lepideus Fr.	6
Lenzites betulina (Linn.) Fr.	7½
L. striata Swartz (from imported timber)	5
*L. trabea** Pers. (Richards, U.S.A.)	9
Merulius lacrymans (Wulf.) Fr.	9
M. serpens (Tode) Fr.	10
M. tremellosus (Schrad.) Fr.	7
Mycena galericulata Scop.	No fruiting
Panus torulosus (Pers.) Fr.	8 (Ab.)
*Paxillus panuoides** Fr.	6
Phellinus cryptarum Karst.	5
Pholiota adiposa Fr.	7
P. aegerita (Porta) Fr.	11
P. heteroclita Fr.	7½ (Ab.)
P. lucifera (Lasch) Fr. (Mounce, Canada)	No fruiting
P. mutabilis (Schaeff.) Quél.	10½
P. squarrosa (Müll.) Fr.	7
Pleurotus euosmus (Berk.) Cke.	6
P. lignatilis Fr.	12
P. ostreatus (Jacq.) Fr.	6½
P. palmatus (Bull.) Quél.	8
P. ulmarius Bull.	12 (Ab.)
Polyporus anceps Peck (Davidson, U.S.A.)	10
P. balsameus Peck (Mounce, Canada)	8
P. benzoinus (Wahl.) Fr.	7
P. borealis (Wahl.) Fr. (Mounce, Canada)	8½
P. brumalis (Pers.) Fr.	No fruiting
P. dichrous Fr. (Overholts, U.S.A.)	6½
P. frondosus Fr.	6
P. fumosus (Pers.) Fr.	9
P. giganteus (Pers.) Fr.	8
P. gilvus Schw. (Lurie, South Africa)	11
P. obtusus Berk. (Humphrey, U.S.A.)	7
P. picipes Fr.	12
P. radiatus (Sow.) Fr.	12
P. rugulosus Lév. (Lurie, South Africa)	8
*P. Schweinitzii** Fr. (2 strains)	6–7
P. shoreae Wakefield (Bagchee, India)	13
P. sulphureus (Bull.) Fr.	10
P. Tuckahoe (Güssow) Sac. & Trott (Mounce, Canada)	15 (Ab.)
P. tulipiferus (Schw.) Overholts (Mounce, Canada)	10
Polystictus abietinus (Dicks.) Fr.	6
P. cinnabarinus (Jacq.) Cke. (Cummins, Australia)	8
P. hirsutus (Wulf.) Fr.	4½
P. leoninus Klotz. (Bose, India)	6
P. pergamenus Fr. (Mounce, Canada)	10
P. sanguineus (L.) Mey (Bagchee, India)	8½
P. versicolor (Linn.) Fr. (3 strains)	7
Poria incrassata (B. & C.) Burt (Humphrey, U.S.A.)	No fruiting
P. obducens (Pers.) Fr. (Mounce, Canada)	9
P. Rickii (?) (Davidson, U.S.A.)	7 (Ab.)
P. subacida Peck (Mounce, Canada)	12
P. Vaillantii (DC.) Fr.	3
P. vaporaria (Pers.) Fr.	5
P. xantha Lind.	5
Schizophyllum commune Fr.	5½
Stereum hirsutum Fr.	5
S. illudens Berk. (McClennan, Australia)	7
*S. lobatum** Fr. (McClennan, Australia)	11
S. purpureum Fr.	10
S. rugosum (Pers.) Fr.	10
S. sanguinolentum (Alb. & Schw.) Fr.	6½
S. spadiceum Fr.	12
Trametes heteromorpha (Fr.) Bres. (Mounce, Canada)	No fruiting
T. Pini (Brot.) Fr. (2 strains)	No fruiting
T. rubescens (Alb. & Schw.) Fr.	8
T. serialis Fr. (Mounce, Canada)	5
T. violacea Lloyd (Lurie, South Africa)	9

serialis usually fructify on the underside of pieces of wood in the open. *Polyporus Schweinitzii* and *Fomes annosus* usually form sporophores in shaded positions at the base of trees—the latter sometimes on roots in rabbit burrows. By contrast, others, such as *Polystictus versicolor* and *Lenzites sepiaria*, fruit on posts, etc., exposed to full light, and it is logical to expect their light requirements in the laboratory to differ. It is interesting to note that the five agarics which fruit regularly on malt agar in plugged test-tubes in an incubator in the laboratory are species listed by C. Rea as ones which can fructify out of doors in the winter. These are *Collybia velutipes*, *Coprinus micaceus*, *Pleurotus ostreatus*, *P. palmatus* and *Schizophyllum commune*.

Summing up the conditions necessary for the formation in the laboratory of sporophores of wood-rotting Basidiomycetes, the following desiderata appear to be the more important:

(1) The provision of a generous supply of a rich, well-aerated medium; this can be supplied by sawdust of an easily decayed timber, to which readily available nutrients have been added.

(2) A plentiful supply of moisture in the medium.

(3) An atmosphere of moderately high relative humidity, but not a saturated atmosphere, at the surface of the medium and around the developing sporophores. Failure to obtain normal fructifications in culture vessels is often the result of an excessively high humidity within them.

(4) Exposure to light of moderate intensity, the length of exposure and the intensity of the light depending on the species of fungus and usually bearing a relation to its normal ecological requirements.

Summary

Methods are described for cultivating wood-rotting fungi on a medium consisting of sawdust to which various nutrients are added, so as to produce in fairly short periods fructifications which are sufficiently typical of the species to be readily recognized.

The conditions most favourable for the production of sporophores by wood-rotting fungi in culture are briefly discussed, and it is concluded that they include (1) the provision of a rich medium containing readily available food materials in addition to wood substance, (2) plentiful supply of moisture to the substratum, (3) an atmosphere not saturated, but having a fairly high relative humidity, around the developing fruit bodies, (4) exposure to daylight of moderate intensity.

The work described in this report was undertaken as part of the programme of the Forest Products Research Board and is published by permission of the Department of Scientific and Industrial Research.

Notes on table

Beech sawdust was used throughout, except for those species marked with an asterisk, for which Norway spruce sawdust was used. A number of other species were successfully grown on spruce sawdust as well as on beech dust.

Though in by no means all the species tested were the fructifications normal or identical with those formed in nature, yet they mostly showed the typical features by which they could have been recognized had the identity of the culture been unknown. Only in those species where (Ab.) is placed alongside the number in the time column were the fruit bodies abortive or imperfect.

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EXPLANATION OF PLATE VII

Fig. 1. *Pleurotus ostreatus*—sporophores formed from mycelium which has grown through plug: 8 weeks after inoculation. (× $\frac{2}{3}$.)
Fig. 2. *Fomes Clelandii*—fructification formed after 4 months on plug at end of tube after removal from flask. Note strip of wet cotton wool to keep plug moist. (× $\frac{1}{2}$.)
Fig. 3. *Ganoderma resinaceum*—fructification formed at mouth of tube after removal of plug: 12 weeks after inoculation. (× 1.)
Fig. 4. *Merulius tremellosus*—fructification formed at mouth of tube after removal of plug: 7 weeks after inoculation. (× 1.)
Fig. 5. *Pholiota adiposa*—plug removed and tube only half-filled with medium: 7 weeks after inoculation. (× $\frac{1}{2}$.)

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4
2
5

STACHYBOTRYS

By G. R. BISBY, *Imperial Mycological Institute, Kew*

(With 9 Text-figures)

Historical

The genus *Stachybotrys* was founded by Corda (1837; commonly but erroneously cited as dating from his *Anleitung*, 1842) with one species, *S. atra*. The generic diagnosis, translated, is: 'Fertile hyphae ("stipes") septate, branched; branches crowned at the apices with very short, verticillate, mammillate branchlets forming a capitulum; spores two-celled, homogeneous, regularly placed and within the capitulum.' He added a note that this genus with *Dendryphium*, *Puccinia*, *Dicoccum*, and *Didymosporium* constituted a family Stachybotrydeae. His specific diagnosis is: 'St. atra. Mycelial tufts thin, black; fertile hyphae dichotomous, few-septate, olivaceous-yellow; branchlets white above; spores fuscous, ovate, with a thick transverse septum, 0·000340 Pariser Zolles. On walls, Prague, in winter.' The Paris Zoll is equal to 27·9 mm.; that makes the spores about 9·5 μ long. The branchlets are phialides. Corda's figures are reproduced here (Fig. 1).

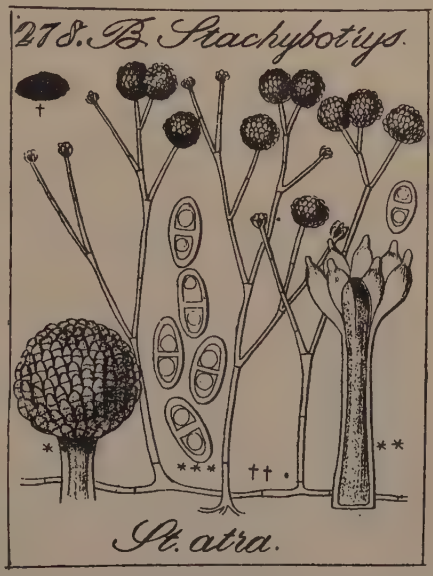


Fig. 1. Corda's figures, 1837. The fungus is shown natural size at †.

Berkeley (1841) described and figured *Sporocybe** *lobulata*, noting that it 'appears to have a great resemblance to *Stachybotrys atra* Corda, but the lobes are not so distinct; neither are they mammillate, and the sporidia have no true septum'. Later, Berkeley and Broome (1859) recorded *S. atra*, remarked that its spores 'are not in any stage echinulate, nor are they so broad' as those of *Sporocybe lobulata*, 'which evidently belongs to the same genus', and the next year Berkeley (1860) placed the latter under *Stachybotrys*.

In the meantime Bonorden (1851) had described and figured *S. alternans* (Oudemans later drew the better-known but rather schematic illustration). Then Saccardo and Cooke each added a couple of species of doubtful status. Grove (1886) described *S. dichroa* with spores stated to be one-

* *Sporocybe* sensu Berkeley did not have synnemata.

septate but figured as biguttulate. A description sent to Saccardo appeared in *Sylloge* IV before Grove's own publication.

Thus *Stachybotrys* in 1886 had eight so-called species, six of which had one-celled spores and two (including what is now known as the type) were said to have two-celled spores. Saccardo compiled the genus in the Dematiaceae-Amerosporae, and added '(spurie?)' before each mention of '1-septatis'. The dozen specific names added since 1886 have all applied to specimens with one-celled spores. Saccardo had fixed the generic concept: not from any 'type species' but from all the species he knew. He did not know, nor do we know, a genus with one-septate spores but in other ways like the fungus that had come to be known as *Stachybotrys*, a name still universally used for a common fungus on old plant material including damp paper, cotton, and linen; it may cause commercial damage (see Sée, 1919; Thaysen & Banker, 1927; G. Smith, 1938).

Von Höhnel (1923), in some notes published posthumously, argued that *Stachybotrys* Corda referred to a fungus which grew on walls, had two-celled spores, and had never been found again; that *Stachybotrys* of subsequent authors grew especially on paper, had one-celled spores, and must be renamed. He guessed that the name *Memnonium* Corda could be used, reported that the type of *Synsporium* Preuss was a species of what had been called *Stachybotrys* but must now be called *Memnonium*, and gave the following synonymy:

Memnonium effusum Corda, 1837

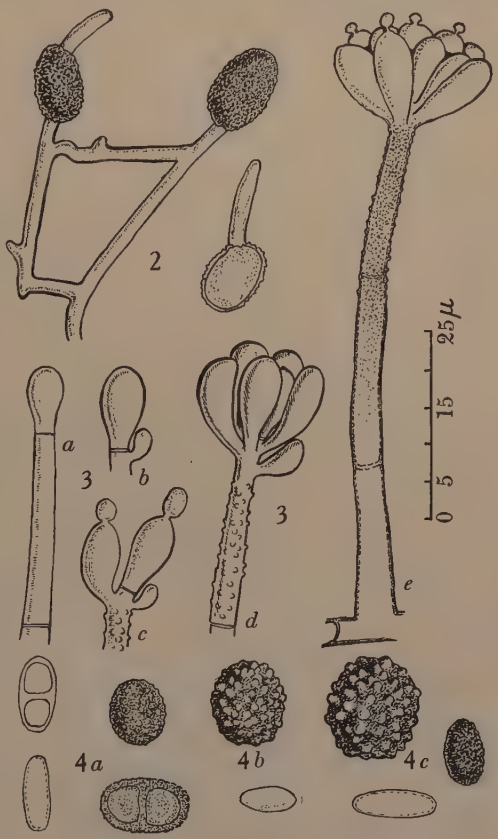
Synsporium biguttatum Preuss, *Aspergillus alternatus* Berk., *Sporocybe Desmazieri* Corda, *Sporocybe lobulata* Berk., *Stachybotrys alternans* Bon., *Memnonium sphaerospermum* Fuckel.

This is a curious mixture of sense and nonsense. Corda's figure and description of *Memnonium effusum* might refer to many a fungus, but there is no indication that it had the distinctive phialophores and phialides which Corda figured the same year for his *Stachybotrys*. There is no type material, and Saccardo's guess that *Memnonium* was a *Trichosporium* might better stand. Corda's figures of *Sporocybe Desmazieri* do not look much like *Stachybotrys*. How did von Höhnel know that there was no paper (or other cellulose) on the wall from which *S. atra* came, or that the spores were really two-celled? He did not examine the type specimen, which was later reported (Pilat, 1938) to be in Prague. Until such examination may be possible, it seems much more reasonable to assume that Corda's specimen has non-septate spores, for (see below) many fresh, biguttate spores appear septate.

Observations on cultures, specimens, and nomenclature

A score of specific names has been applied to *Stachybotrys*, but only three—*S. atra*, *S. lobulata*, and *S. alternans*—are commonly reported. Of these three, type material of *S. lobulata* only is available to me at the moment, but type specimens of a half dozen other 'species' have been examined. First, however, a few terms need mention, then cultures such as may readily be obtained will be described.

The conidiophore is a compound structure in *Stachybotrys*, for which these terms are here used (see Figs. 3, 5): *phialides*, the structures which produce the conidia; *phialophore*, the 'simple conidiophore' distinctive of the genus, with its crown of phialides at the apex; *compound phialophore*, the 'branched conidiophore' which consists of the primary phialophore and one or more secondary phialophores arising as branches. For mycelial aggregations these terms are used: *strands*, decumbent groups of parallel or intertwined hyphae; *ropes*, erect, conspicuous hyphal structures which may simulate synnemata or coremia on rich media such as malt agar, being up to 5–10 mm. high and 1 mm. wide at the base, tapering upward. These ropes of hyphae generally occur in groups. The term 'synnema' is not used here because that suggests the Stilbaceae; *Stachybotrys* belongs to the Dematiaceae.



Figs. 2–4. *Stachybotrys atra*. 2, germinating spores and formation of hyphal anastomoses. 3, stages in development of phialides: the simple phialophore 3*e* is indicated in optical cross-section. 4*a*, spores, young and old, of the Nottingham isolation, showing range and guttae. 4*b*, two spores showing range in the culture Timonin 1803. 4*c*, three spores showing range in the type specimen of *S. scabra* Cooke & Harkn. All × 1000.

Culture 1. Isolated late in 1941 from rotting canvas, Nottingham, and sent to Miss E. M. Wakefield. —A spore germinates by one or two germ tubes which break through the spore wall, generally near one or both ends (Fig. 2). The young hyphae anastomose and form a hyaline mycelium which grows about 1 mm. in radius each day at room temperature. Strands are formed on the surface of the medium. Within a week conidiophores and conidia develop and turn dark, giving to spore-producing areas a dull, inky-black appearance, often with glistening droplets of slime. In older cultures the vegetative hyphae may show a tinge of olivaceous.

A primary phialophore rises from a hypha—a simple hypha or one in a strand or a rope. The apex swells, then becomes cut off by a septum to form the first phialide; meanwhile one or two septa develop along the phialophore (Fig. 3; Zopf, 1890, gives good figures). The first phialide produces an apical bud which grows into a conidium, while four or five

more phialides form successively in a circle below the first; only the apical phialide seems to be cut off by a septum. Meanwhile the phialophore becomes roughened, and soon the phialides also. The conidia turn dark while still immature, and the apex of the phialophore also becomes olivaceous as the spores develop. Then another circle of four or five phialides may form in succession below the first whorl, making a compact crown surmounting the phialophore. Each phialide produces conidia (slime spores) in succession until a head of fifty or more collects, held in a cluster by slime. Frequently two or more clusters combine.—A mature phialophore is olive brown, especially above, about 5 μ wide at the base and 3 μ at the apex, of varying length, commonly 50–100 μ. A secondary phialophore frequently develops as a branch from the primary, and so on, forming a compound phialophore (Fig. 5) with more or less definite alternate branching.

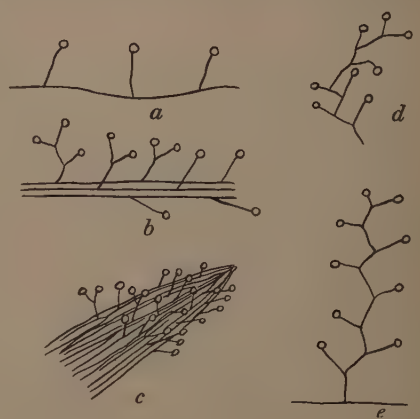


Fig. 5. Diagrams of arrangement of phialophores of *Stachybotrys atra*: *a*, simple or primary phialidophores arising from a hypha; *b*, simple and compound phialophores from a strand and *c*, from a rope; *d*, *e*, the usual alternate arrangement of phialophores.

The phialides are 10–15 × 5–7 μ, obovate or pyriform, becoming roughened and olivaceous. Corda's description of them as 'mammillate' refers to the young spores at the apices. A mature phialide in water may put out a hypha. The phialides are not deciduous, but eventually collapse *in situ*. Phialides are generally (and by definition) flask- or ninepin-shaped cells, cut off by septa. It seems to us, however, that the term phialide should be used for the spore-producing organs of *Stachybotrys*, despite their shape and the lack of distinct septa except beneath the terminal phialides.

The conidia (Fig. 4*a*) first abstricted are 8–11 × 3·5–6 μ, smooth or nearly so, translucent olive brown. In older cultures many of the spores are conspicuously roughened; wider (8–12 × 5–7·5 μ; some are subglobose), and many are opaque and black. The translucent spores, in young or old cultures, show none, one, three or, most commonly, two guttulae; the latter are often so placed as to lead an observer to think the spores two-celled until he makes appropriate tests, which show that they are non-septate. Under Corda's microscope, such spores would seem definitely septate.

Several single-spore cultures were made, but there was no obvious difference, macroscopic or microscopic, between them. When these cultures were about a month old, most of them (and less commonly mass transfers) showed a pale, more or less spreading, hyphal overgrowth which suggested a contaminant or a parasite. Transfers from this overgrowth demonstrated that it belonged to the *Stachybotrys*; successive transfers from

it soon produced colonies nearly or quite sterile, some with a salmon-pink colour, others nearly white. This is another example of the dual phenomenon (Hansen, 1938; see also Presley, 1941), and explains why the fungus may seem to 'run-out' if transferred from older cultures bearing overgrowth.

Culture 2. An isolation from soil, Canada (M. Timonin No. 1803), differed only in having some spores even narrower in young cultures, where they were 8–10 × 3–5 μ, but even wider (8–11 × 5–10 μ, many globose, rough, and opaque) in cultures a month old (Fig. 4*b*).

Culture 3. Another soil culture (isolated 1939, G. Smith No. 158) differed from the Nottingham fungus in having earlier and more pronounced darkening of the phialophores and phialides.

Four other isolations were studied, but all fell within the range shown by the three mentioned above. The seven cultures evidently belonged to one and the same species.

What name should be applied to this common and widespread species? Examination of the type specimen shows that it can be called *Stachybotrys lobulata* (Berk.) Berk., a name we have commonly used in the past. However, since Corda's figures and description make it almost certain that his species was the same, *S. atra* Corda is used here to obviate the future necessity of changing to his name when and if his type is re-examined. In the very unlikely chance that his type proves to be different, then *Stachybotrys* obviously should become a *nomen conservandum propositum* in the sense now universally accepted.

As noted above, Berkeley recorded *Stachybotrys atra* in 1859. The specimen he examined is marked by him 'Sporocybe lobulata with Stachyb. atra Batheaston March 1859'. It is evident from a glance at this specimen and from Berkeley's remarks quoted above that he considered the young stage of *Stachybotrys* to be *S. atra*, the older to be *S. lobulata*. There would still be ample justification for two or more specific names were it not that single-spore cultures prove that there is variability, especially between spores in young and in old cultures. The 'fathers of mycology' cannot be blamed for basing names on what seemed to them good specific characters.

The first specific epithet after Corda's which applies to the common *Stachybotrys* appears to be that of *Aspergillus alternatus* Berk. (1838). Berkeley transferred it to *Sporocybe* in 1841 and reported that it was nearly allied to *S. lobulata*. Apparently no one has transferred *S. alternata* to *Stachybotrys* (Saccardo made it a *Periconia*). As von Höhnel (1923) reported, the type specimen is the same species as *S. lobulata*, herein considered *S. atra*.

There is no feature of the original description or figure of *Stachybotrys alternans* Bon., which constitutes a basis for a distinct species. Both *S. scabra* Cooke and Harkness (Fig. 4*c*) and *S. verrucosa* Cooke and Massee are well developed *S. atra*; the type (and only) specimen of each in Kew Herb. has ellipsoid, smooth, pale young spores 4 μ wide as well as very rough, opaque, subglobose spores up to 14 × 12 μ. *S. asperula* Massee, correctly redescribed by Petch (1931) (his 'catenulate' means that the spores arise successively from phialides. They are not in chains), is also mature *S. atra*. The

paper substratum came from Ceylon, but there is no assurance that the fungus did.

Pending study of the type specimens by future workers, we may gather from the descriptions or figures that the following were probably *Stachybotrys atra*: *S. atrogrisea* Ell. and Everh. (the authors stated that it might be a 'variety' of *S. atra*), *S. gracilis* Ém. March., *S. elasticae* Koord. and *S. dakotense* Sacc. The following are possibly *S. atra*: *S. pulchra* Speg., *S. cylindrospora* Jensen, and *S. Voglinii* Cif.

Species belonging to the so-called subgenus *Sterigmatobotrys* (which was first proposed by Oudemans in 1886 as a genus), viz. *Stachybotrys elata* Sacc., *S. papyrogena* (Sacc.) Sacc., and *S. socia* (Sacc.) Sacc., apparently do not belong in the genus *Stachybotrys*, but I have seen no authentic or other specimens. Costantin in 1888 proposed the genus *Phragmostachys*, said to be based on '*P. atra*', but his figures show that 'atra' is a lapsus calami for 'elata'; *Phragmostachys* is a synonym of *Sterigmatobotrys*.

The diagnosis and figures of *Stachybotrys elongata* Peck indicate that the fungus is not a true *Stachybotrys*.

Cooke (1883) described '*Stachybotrys sub-simplex*, *Cooke*, *Rav. Amer. Fungi*, No. 775. Effusum, atrum. Hyphis simplicibus, erectis, tenuibus, septatis, superne lobato-capitatis. Sporis globosis, laevibus, atrofuscis (·006 mm. diam.). On *Musa* (Rav., 3368). Darien, Georgia.'

This species has heretofore been reported from the one collection only.* The type specimen is marked by Ravenel '3368 on leaves of banana (Musa) Darien Ga. Nov. '81 H.W.R.' Cooke's copy of Ravenel *Fungi Americani Exsiccati* 775 is marked in ink '3368'. There is a good development of an effuse, sooty-black mould. The septate hyphae are pale brownish, 2–4 μ wide. The phialophores are somewhat roughened, 4–6 μ wide, up to 200 μ or more long, darker than the hyphae, simple (so far as noted, i.e. arising from the hyphae, not from other phialophores), crowned above by five to ten pyriform or ellipsoid phialides 10–12 × 4–6 μ. Conidia globose or subglobose, five to nine (mostly six to eight) μ, formed in clusters on the phialides (Fig. 6).

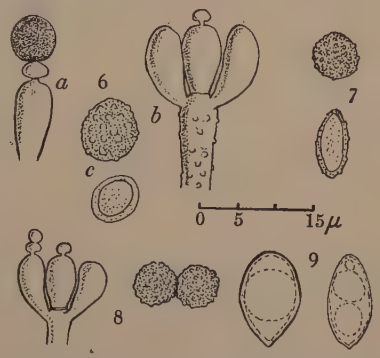
On the same herbarium sheet in Kew Herb. is affixed a Californian specimen '2229 On Agave. Harkness' to which Cooke has added sketches of roundish, dark spores and a note: '*Stachybotrys* (?) too sandy to examine properly'. The rough surface of the leaf and the black fungus are coated with very fine sand grains. After a little manipulation, phialophores of *Stachybotrys* were revealed; these were 3–4 μ wide, somewhat roughened, pale with a tinge of olive, bearing a crown of phialides 10–12 × 5 μ, with conidia globose to oval, 4–6 (7) × 3–4 μ.

To supplement these two dried specimens, we received in 1937 cultures (since lost) and slides of a *Stachybotrys* isolated by Dr G. R. Bates from citrus fruit washings, Southern Rhodesia. The colonies were hyaline, then dull greenish black from the conidial masses. Hyphae hyaline, 2 μ (or less) wide, often aggregated into strands; phialophores typically simple, erect, one to three septate, inconspicuously roughened, 40–50 μ long, 3–5 μ wide

* Fig. 172 in Wardlaw's *Diseases of the Banana*, 1935, is of *S. subsimplex*, though by accident labelled *Haplographium*.

and hyaline at the base, becoming pale fuscous above, about 2 μ wide at the apex which bears up to ten obovate phialides which are 6–10 × 3–4 μ, straight or curved, hyaline becoming brownish; conidia formed in clusters, variable, globose and 3–6 μ or oval and 4–10 × 3–4 μ, becoming opaque black and somewhat roughened (Fig. 7).

This fungus in culture showed variability comparable with that of *Stachybotrys atra*, but the phialophores were generally simple, the spores smaller and often globose even in young cultures. Pending further collections, we are using the name *S. subsimplex* for the two herbarium specimens and Bates's cultures.



Figs. 6–9. 6, From the type specimen of *Stachybotrys subsimplex*: *a*, phialide with one young spore and one nearly mature; *b*, young phialophore bearing three young phialides; *c*, mature spore in surface view and young spore in optical section. 7, Two spores from Bates 239, considered to be *S. subsimplex*. The phialides are like those shown in Fig. 6. 8, Tip of young phialophore and two spores from *Memnoniella echinata* (Riv.) Galloway. 9, Two spores of the 'pink *Stachybotrys*' from Canada. All × 1000.

We now mention *Gliobotrys*, founded by von Höhnel (1902) for fungi like *Stachybotrys* except in having hyaline fertile hyphae [phialophores]. The type species, *Gliobotrys alboviridis* on decayed wood, was described with conidia 4–6 × 3–4·5 μ. It seems possible that the fungus was *Stachybotrys subsimplex* as here interpreted.

As a second species of *Gliobotrys*, von Höhnel transferred *Stachybotrys dichroa* Grove because its conidiophores were said to be hyaline. An examination of a bit of Grove's type shows, however, that it is young *S. atra*; some of the phialophores have a tinge of olivaceous. In any event, two distinct genera are not needed for Dematiaceae alike except that one has hyaline phialophores which become dark, the other phialophores which are supposed to remain hyaline.

Late in 1937 we received from Dr J. E. Machacek (his No. 408) a fungus isolated from soil, Winnipeg, which is more than a *Gliobotrys*; it is definitely one of the Moniliaceae, being salmon pink on most media. No dark tinge has ever been seen in any part of the fungus. It grows vigorously (a culture fifty-one months old promptly revived when melted agar was added) and produces masses of slime-spores 10–12 (13) × 5–8 μ on phialides on roughened phialophores. In other words, the fungus is like *Stachybotrys* except in colour; indeed, it is like *S. atra* except in colour, in its slightly longer (12–17 μ) phialides, little branching of phialophores, and in its spores which are somewhat pointed at one or both ends (lemon-shaped to broadly fusiform, fig. 9), generally with only one large guttule, and remaining smooth or nearly so.

At first thought it seems obvious that this fungus requires a genus in the Moniliaceae since, in Saccardo's classification, colour determines the family. Since no genus seems to fit, a new one is indicated, unless one begs the question by 'emending' *Gliobotrys* out of the Dematiaceae.

Upon second thought, it seems strange that no one has ever reported such a fungus, for most soil moulds are widely distributed. It came from the centre of North America, not from unknown Tibet. How much of this fungus is known 'in nature'? The progeny of one spore only is known to us, a spore isolated by dilution plates from soil that is exposed to frigid winter and the heat and ultra-violet rays of summer; a spore that had to submit further to several laboratory manipulations before it developed its first bizarre, pink colony. No; there are already too many genera based on freaks. Furthermore, we managed to isolate from typical *Stachybotrys atra* a mycelioid growth of the identical pink colour. In view of the differences noted above, and of failure to get fusions between germ tubes from *S. atra* and from the pink fungus, we cannot call the latter 'pink *S. atra*'; but we propose to call it 'pink *Stachybotrys*' until there is more evidence that Nature has definitely added such a fungus to her flora.

Memnoniella von Höhnel (1923) requires a word. It was described as differing from *Stachybotrys* (as '*Memnonium*') in having catenulate spores. Galloway (1933) obtained a fungus which was found to agree with von Höhnel's type specimen; like the type, it came from cotton yarn. Since an earlier figure and description by Rivolta seemed to refer to the same fungus, the combination *Memnoniella echinata* (Rivolta) Galloway was made.

Galloway's isolation, which has now been ten years in culture, was obtained from the Lister Institute. There is little to add to Galloway's description. The mycelium is salmon-pink like that of the overgrowth of *Stachybotrys atra* mentioned above and, on rich media, produces strands and numerous small, erect ropes of hyphae. Spore production is now somewhat reduced; phialophores unbranched, conidia rough-globose, 4–5 μ, in chains which readily break up, sometimes forming clusters (Fig. 8).

Memnoniella is a suspiciously rare fungus, with two definite records and one probable, all from Europe (though the two on cotton yarn may, of course, have been introduced with the cotton). We can add another; we have a slide made from a culture isolated by G. R. Bates, Southern Rhodesia, with spores somewhat disk-shaped, 4·5–5·5 × 3–4 μ in the chains, i.e., in side view, and 4·5–5·5 μ when flat. The chains are rather persistent.

We suggest the possibility that *Memnoniella echinata* may be *Stachybotrys subsimplex* with slime production reduced sufficiently to allow the retention of spores in chains. Galloway's fungus was a single colony from 'cotton yarn, heavily mildewed with *Stachybotrys* sp., and kept for some years in a sealed jar'; Bates's isolation was from the citrus washings which produced several cultures we called *S. subsimplex* above. Several fungi, including *Gliomastix* (which has similarities with *Stachybotrys*, see Mason, 1941) and *Trichoderma* (Bisby, 1939), may produce spores in heads or in chains, depending on conditions.

Summary of taxonomy and nomenclature of *Stachybotrys* Corda, 1837

Hyphae, phialophores, and phialides hyaline, brightly coloured, or dark; strands or ropes of hyphae may be produced. Conidia (slime-spores) one-celled, normally dark and accumulating into a cluster. The distinctive

characteristic of the genus is the septate phialophore or simple conidiophore bearing a crown of phialides and generally becoming dark. A phialophore arises directly from a hypha or, frequently, from another phialophore. Perfect stage unknown.

Synonyms: *Synsporium* Preuss, 1851, fide von Höhnel.
?*Gliobotrys* von Höhnel, 1902.

The two species recognized by the writer and described in some detail above are summarized here:

(1) *Stachybotrys atra* Corda, 1837

Synonymy, excluding nomenclatural synonyms: *Aspergillus alternatus* Berk., 1838; *Sporocybe lobulata* Berk., 1841; *Stachybotrys alternans* Bon., 1851 (presumably); *Synsporium biguttatum* Preuss, 1849 and 1851, fide von Höhnel; *Memnonium sphaerospermum* Fuckel, 1869, fide von Höhnel; *Stachybotrys scabra* Cooke & Harkness, 1884; *S. dichroa* Grove, 1886; *S. asperula* Massee, 1887; *S. verrucosa* Cooke & Massee, 1888; ?*S. atrogrisea* Ellis & Everh., 1888 (type not seen); ?*S. gracilis* Ém. Marchal, 1894 (type not seen); ?*S. elasticae* Koord., 1907 (type not seen); ?*S. dakotense* Sacc., 1917 (type not seen); *S. pulchra* Speg., *S. cylindrospora* Jensen and *S. Voglinii* Cif. are possible synonyms.

Each phialophore may produce another as a branch; phialides 10–16 × 5–7 μ; conidia 8–12 (14) × 4–9 (12) μ, elliptical to oval on younger growth of the fungus, often subglobose on older growth.

(2) *Stachybotrys subsimplex* Cooke, 1883, tentatively emended. *Gliobotrys alboviridis* von Höhnel, 1902, may be a synonym; *Memnoniella echinata* (Rivolta) Galloway, 1933, is similar except in having catenulate spores.

Phialophores generally simple; phialides 6–12 × 4–6 μ; conidia globose, 3–9 μ or elliptical, 4–10 × 3–5 μ.

Doubtful species: *Stachybotrys crassa* Él. March., 1895. Conidia globose, 16–18 μ. One collection on dung, Belgium. Marchal's figure of a phialophore indicates that he had a *Stachybotrys*, but until the type specimen can be examined, or the species rediscovered, *S. crassa* must remain somewhat doubtful.

Excluded species: *Stachybotrys elata* Sacc., *S. papyrogena* (Sacc.) Sacc., *S. socia* (Sacc.) Sacc., *S. elongata* Peck.—Von Höhnel (1912) suggested that the following might belong to *Stachybotrys*: *Periconia amphispora* (Bon.) Sacc., *P. digitata* (Cooke) Sacc. and *P. minima* (Cooke) Sacc. The type of *P. minima* is not a *Stachybotrys*. No specimen of *P. digitata* has ever been placed in Kew Herbarium. No material of *P. amphispora* has been seen by me.

Discussion

This paper is intended as a small contribution toward the large amount of synthesis still to be undertaken in the taxonomy of fungi. No matter how much a 'splitter of species' one may be by inclination, he cannot ignore the variability manifest in cultures started from a single spore. We have

not ascertained how or why the spores in a young culture of *Stachybotrys atra* are elliptical, translucent, and nearly smooth, whereas many of those in an older culture are rounded, opaque, and rough; but we are sure of the fact, and that the same sequence occurs in the field. Not only do the spores vary, but also the hyphae, phialophores, and phialides. Two or three early names were proposed, rightly for those days, on such variants; a dozen other names have merely accumulated during a century of emphasis on analysis in the taxonomy of fungi. *S. atra* is the only common species in north temperate regions; it has eight specific names still recognized in British literature: six under *Stachybotrys*, *Aspergillus alternatus*, and *Synsporium biguttatum* (Dale, 1914). Certain other countries have even more names for the fungus.

Stachybotrys subsimplex is here interpreted as the second good species of the genus. It is a saprophyte apparently of warmer regions. It is suggested that possibly both *Gliobotrys* and *Memnoniella* were based on this species or variants of it: whatever their status their apparent rarity casts suspicion upon them.

In current taxonomic literature there are thousands of specific and hundreds of generic names which only confuse; some of them were certainly based on mere freaks, and many on hasty or careless work. One may propose, as in this paper, to reduce a few names to synonymy; but there is no way to eliminate a name, once published. Generic names are particularly in need of synthesis and rationalization; more than seven thousand have been proposed for fungi.

The writer, being an old offender, is in a position to remark that local lists of fungi, though often useful, provide human temptation to add 'new records'. I recorded *Stachybotrys* '*cylindrospora*' and '*S. lobulata*' from Manitoba; but the brief notes added make it clear that one was young, the other old, *S. atra*. Similarly, the second record of *S. dichroa*, published by Crossland, refers to a specimen marked *S.* '*dichroa* Grove plus a few other things. On dead stem of *Epilobium*.' There is no *Stachybotrys* evident under a lens, but Crossland's coloured drawing indicates that there had been a bit of pale, young *S. atra*.—It must be said, however, that both Crossland and I had to rely on analyses, for there was no synthesis of the genus *Stachybotrys*.

Summary

1. *Stachybotrys*, with twenty specific names in current literature, is considered to have two distinct species. *S. atra* is a common mould in north temperate regions, and probably elsewhere. *S. subsimplex* is not well known; we have seen two dried specimens and two or three cultures, all from rather warm areas, which we interpret as belonging to it.

2. *S. atra*, and evidently *S. subsimplex* also, are variable in culture and in the field.

3. *Gliobotrys* has no good distinguishing character. It is suggested that *Memnoniella* and a 'pink *Stachybotrys*' may be unusual or abnormal developments of *Stachybotrys*.

4. A plea is made for synthesis in mycological taxonomy.

Grateful acknowledgment is made to E. W. Mason and other workers at the Imperial Mycological Institute, to Geo. Smith, to Miss Wakefield and the authorities at the Royal Botanic Gardens, Kew, for suggestions and cultures, and the privilege of examining type specimens. Transfers of the '*pink Stachybotrys*' and the Nottingham isolation of *S. atra* have been sent to the National Collection of Type Cultures.

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AN ABNORMAL GROWTH ON MUSHROOMS

By W. A. R. DILLON WESTON and R. ERIC TAYLOR

(With 1 Text-figure)

A bed of mushrooms was grown by one of us on the concrete floor of a disused garage. The bed was prepared, cased and spawned in the orthodox way, with the exception that the depth of compost was rather shallow so that on various occasions it was necessary to apply water. There was relative freedom from fungal and insect pests, but slugs frequently invaded

Fig. 1.

the bed. Excellent yields were obtained and no abnormalities of growth were noted with the exception of one fructification (Fig. 1). A slight corrugation was noted on the pileus of this when it was about the size of a chestnut, and this developed into a knob-like intumescence which, a fortnight later, had attained the dimensions shown in the illustration. The

peculiar folds and convolutions of this knob-like excrescence, resembling somewhat a rose-comb found in some breeds of poultry, consisted of a hymenium bearing basidia and basidiospores. The gills on the under-surface were normal. It was thought that this abnormal condition might have been caused by some slight mechanical irritation to the skin of the pileus, but attempts to reproduce the condition by scratching the surface of a number of caps with a sterilized needle failed. Reference to the literature showed that a similar condition had been described by Lambert (1930), and referred to by Messrs Darlington and Sons, Ltd. (1934) and Brockhuizen (1937), the term applied to it being the 'rose-comb' disease. Lambert (1930) correlated the incidence of this disease with the use of some form of mineral oil in the mushroom houses, and Brockhuizen (1937) induced it by the use of oilstoves or by the fumes of coal-tar creosote. These mushrooms were grown in a garage where oil had been stored, a condition which (according to the above writers) might be conducive to the disease. Berkeley (1836) described 'a most extraordinary and beautiful state of *Agaricus campestris*', and referred later (1860) to a somewhat similar condition observed in several species of *Agaricus* in which 'an hymenium is produced on top of the pileus as well as beneath...'. Teratological specimens of *Collybia* spp. have been described by Buller (1924) and Ramsbottom (1933) and of *Coprinus ephemerus* by Keyworth (1942), and the nature of these appears to be somewhat similar to that described in the present specimen. We are indebted to Mrs W. A. R. Dillon Weston for bringing this specimen to our notice.

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NOTE ON THE OCCURRENCE OF *OPHIOBOLUS GRAMINIS* SACC. VAR. *AVENAE* E. M. TURNER IN SCOTLAND IN 1942

By S. D. GARRETT, *Rothamsted Experimental Station, Harpenden*, and R. W. G. DENNIS, *Seed Testing, Plant Registration and Plant Pathology Station, Corstorphine, Edinburgh*

The occurrence of *Ophiobolus graminis* Sacc. var. *Avenae* E. M. Turner in the Tweedside area of Scotland has already been reported by Dennis and Foister (1942). During the past season, we were able to search more extensively for this fungus, which we found to be widely distributed in the counties of Ayr, Kincardine and Aberdeen; we also found the disease in the counties of Fife and Banff. We did not find the disease either in the Lothians or Tweedside, the area from which it was first reported by Dennis and Foister (1942), but crops in these districts were not examined until too late for easy detection of Whiteheads. No search was made in areas other than those listed above.

Measurements were made of the length of fifty ascospores from each of twenty-one collections of diseased material obtained on this survey, viz. eleven from Ayr, five from Aberdeen, four from Kincardine, and one from Fife; the fifty ascospores were selected at random from groups of perithecia taken from several stem-bases in each collection. The data substantiate Turner's (1940) claim that *O. graminis* var. *Avenae* can be distinguished from *O. graminis* proper by difference in mean ascospore length. Whereas mean ascospore length in *O. graminis* proper rarely varies outside the range 70–90 μ, the means recorded by Turner for *O. graminis* var. *Avenae* on field material ranged from 101 to 117 μ. So far, no further data on ascospore length in *O. graminis* var. *Avenae* have been reported; all the original measurements recorded by Turner were made on material collected in North and Central Wales, so that our measurements made on the Scottish collections are deemed of sufficient value for publication (Table 1).

Mean ascospore length in the different collections varied from 96 to 119 μ, a range which exceeds only slightly that reported by Turner (101–117 μ). Modal length varied from 95 to 116 μ; in twelve out of twenty-one collections, modal length of the fifty-spore samples was identical, viz. 105 μ. These data thus support Turner's separation of *O. graminis* var. *Avenae* from *O. graminis* proper, on the basis of differences in ascospore length as well as in host range.

The first authenticated reports of the occurrence of *O. graminis* var. *Avenae* outside Wales were made in 1940 by Mr N. C. Preston, from Sidbury in Shropshire, and by Dr F. T. Bennett, from Threlkeld in Cumberland; mean ascospore lengths, determined from material supplied by Mr Preston and Dr Bennett to the senior writer, were $105 \pm 1{\cdot}4$ and $123 \pm 0{\cdot}8$ μ respectively. So far, the Whiteheads disease of oats has not

been reported from areas outside those in which oats are the chief cereal crop. The association of this disease with consecutive oat cropping was noted by us in Ayr, where it is the practice to take two, and occasionally three, consecutive crops of oats after ploughing up old grass. This apparent restriction of *O. graminis* var. *Avenae* to areas in which oats is the dominant cereal is somewhat difficult to explain, in view of Turner's finding that this variety of the fungus could attack wheat and barley as well as oats, though it is true that infection of these hosts in her experiments was not as vigorous as that by *O. graminis* proper. A more careful search for *O. graminis* var. *Avenae* in the south and east of England must now be undertaken; at the same time, ascospore measurements should be made on collections of wheat and barley attacked by the Take-all disease in Scotland, Wales and the north-west of England, since *O. graminis* var. *Avenae* has not yet been found on these hosts in the field, and conclusions as to their susceptibility are based solely on Turner's inoculation experiments. In this connexion, a further observation from our survey is pertinent; oats infected by *O. graminis* var. *Avenae* (mean ascospore length $112 \pm 1{\cdot}2\,\mu$) was discovered at Craibstone, Aberdeen, but wheat suffering from Take-all on another field of the same farm was found to be infected by *O. graminis* proper (mean ascospore length $71 \pm 1{\cdot}1\,\mu$).

We are much indebted to Dr David Clouston, Botanist to the North of Scotland College of Agriculture, and to Mr Laird, Agricultural Organizer for the County of Ayr, for assistance in making this survey of oat crops.

Table 1. *Ascospore measurements in* μ

Origin of sample	Mean length	Modal length	Range in length
Ochiltree, Ayr	$119 \pm 1{\cdot}8$	116	97–176
Ochiltree, Ayr	$102 \pm 1{\cdot}2$	105	84–118
Ochiltree, Ayr	$110 \pm 1{\cdot}0$	109	95–126
Ochiltree, Ayr	$107 \pm 0{\cdot}9$	109	92–123
Ochiltree, Ayr	$103 \pm 1{\cdot}1$	105	80–116
Auchinleck, Ayr	$104 \pm 1{\cdot}1$	105	84–118
Auchinleck, Ayr	$102 \pm 1{\cdot}0$	105	84–116
Tarbolton, Ayr	$109 \pm 1{\cdot}5$	105	78–126
Ayr	$101 \pm 1{\cdot}0$	105	82–116
Maybole, Ayr	$105 \pm 1{\cdot}4$	105	86–126
Dalrymple, Ayr	$105 \pm 1{\cdot}3$	105	84–126
Ceres, Fife	$105 \pm 1{\cdot}8$	105	78–134
Glenbervie, Kincardine	$108 \pm 1{\cdot}1$	105	97–126
Fetteresso, Kincardine	$106 \pm 0{\cdot}9$	105	90–122
Fetteresso, Kincardine	$108 \pm 0{\cdot}9$	105	95–120
Banchory Devenick, Kincardine	$112 \pm 1{\cdot}2$	116	90–132
Newhills, Aberdeen	$112 \pm 1{\cdot}2$	107	97–132
Kintore, Aberdeen	$114 \pm 1{\cdot}0$	115	99–126
Inverurie, Aberdeen	$102 \pm 1{\cdot}4$	101	76–116
Huntly, Aberdeen	$96 \pm 1{\cdot}3$	95	74–116
Cairnie, Aberdeen	$110 \pm 0{\cdot}8$	109	95–126

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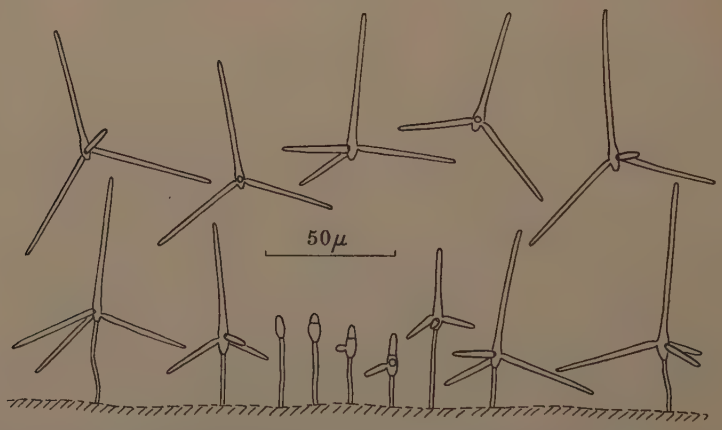
TRISCELOPHORUS MONOSPORUS N.GEN., N.SP., AN AQUATIC HYPHOMYCETE

By C. T. INGOLD, *Department of Botany, University College, Leicester*

(With Plate VIII and 3 Text-figures)

During a brief visit to Reading in September 1942 a collection of submerged decaying leaves of various trees and shrubs was made from a rapidly flowing branch of the River Loddon at Swallowfield. Rich crops of aquatic Hyphomycetes were observed on these leaves, and, of the sixteen species discussed in a previous paper (Ingold, 1942), ten were noted. In addition, on a leaf, too rotten to be identified, the new fungus which is the subject of this paper was observed together with three other aquatic Hyphomycetes (*Clavariopsis aquatica* De Wild., *Tetracladium Marchalianum* De Wild., and *Lunulospora curvula* Ingold).



Text-fig. 1. Above: five liberated conidia. Below: nine conidiophores; the five in the middle have young spores and are arranged to show successive stages in development; the other four conidiophores bear mature spores. The substratum is shown diagrammatically. No cell contents are shown. Drawn with the aid of a camera lucida from living specimens.

The mycelium of the fungus ramifies in the tissue of the decaying leaf, and the conidiophores project at right angles into the water (Text-fig. 1 and Plate VIII, figs. 1, 6). The conidiophores are simple, 15–45 μ long, 1·5 μ wide, and the width is uniform along the entire length. Each bears a single terminal conidium of the aleuriospore type.

On the decaying leaf hundreds of conidiophores were examined with conidia at all stages of development, and from these it was easy to build up in detail a picture of conidium development (Text-fig. 1). This picture was later fully confirmed by actual observations of the course of individual conidium development using the hanging-drop method (Text-fig. 2). The

conidium starts as a small oval swelling at the end of the conidiophore. This spore primordium is soon cut off by a cross-wall. As it elongates it becomes unequally two-celled so that at this stage it looks rather like a conidium of *Venturia inaequalis*. The upper cell of the primordium continues to elongate by apical growth. Soon, from the middle of the lower cell, a small protuberance appears and grows outwards and slightly downwards as a lateral branch. When this has developed to some extent, a second lateral arises at the same level, but in a direction diverging by approximately 120° from the first branch. Later a third branch arises with the same divergence from each of the other two branches. The tip of the upper cell of the spore primordium and the tips of the three branches continue to grow until the spore is fully grown.

The mature spore thus consists of a main axis, continuous with the conidiophore, and of three divergent lateral branches forming a whorl near the base of this axis. The main axis is 50–70 μ long, 4–5 μ broad at its widest part (at a distance of 3–5 μ from its base), and it is here that the three lateral branches project, each making an angle of about 80° with the conidiophore. From its widest part the main axis tapers to 1·5 μ at its truncate base, and to 1·5 μ at its apex. The septum, which at an early stage divides the spore primordium into two cells, becomes more and more indistinct after the laterals have made their appearance, and in the mature living spore it is usually no longer visible. The lateral branches are 40–50 μ long, 2·0–2·5 μ broad near the base, but taper to 1·5 μ at the apex and are abruptly constricted to 1 μ at the attachment to the main axis.

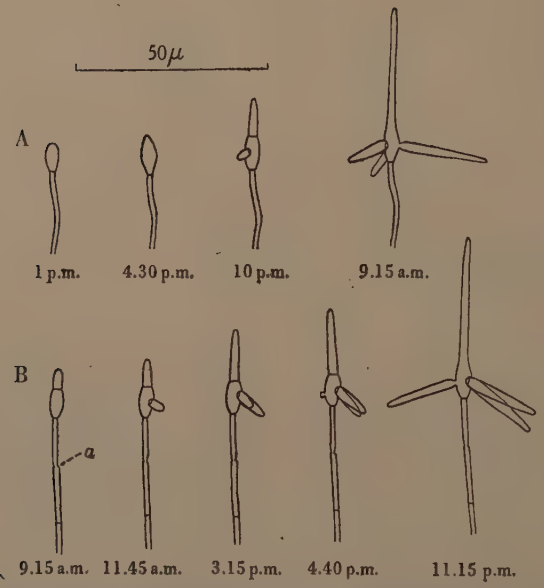
The conidium is liberated as soon as it is fully grown, by separation at the cross-wall between the spore and its conidiophore just as in *Tricladium* spp., *Tetracladium* spp., and *Clavariopsis aquatica* (Ingold, 1942).

The liberation of the spore does not necessarily end the activities of the conidiophore. Thus in the example shown in Text-fig. 2B, a conidium was produced at the point marked *a*. Then, just to the left of this scar left by the first spore, a new hypha grew out from which a new conidium developed.

Hundreds of liberated spores have been examined. They show a great uniformity of structure. The freed spore is highly characteristic. It consists of four long divergent arms of more or less equal length. Of these one is the main axis and the other three are lateral branches. However, since the laterals are not attached at the base but only near the truncate base of the main axis, there is present on the spore a little knob, below the whorl of laterals, representing the basal part of the main axis. It is this little knob which makes the spore so characteristic. It cannot be confused with that of any of the other species of aquatic Hyphomycetes, so far described, which have spores with four long divergent arms (e.g. *Tetracladium Marchalianum*, *Articulospora tetracladia*, *Lemonniera aquatica*, *Tetrachaetum elegans*, *Heliscus longibrachiatus*, *Clavariopsis aquatica*, *Alatospora acuminata*).

The spore germinates readily in water with narrow germ tubes developing from the tips of all four arms (Text-fig. 3). Attempts to get the fungus into pure culture failed.

In comparing this species with aquatic Hyphomycetes previously



Text-fig. 2. Two examples of conidium development as observed in a hanging drop. In B the conidiophore had previously produced a conidium at the point *a*. For details see text. At 3.15 p.m. the second lateral had just begun to develop directly behind the first lateral.

Text-fig. 3. Germination of a spore in water.

described (Ingold, 1942, 1943) it is clear that the species which it resembles most, superficially, is *Lemonniera aquatica*. In most of these aquatic fungi with four-armed spores, the spore is attached to its conidiophore by the end of one of its four arms. This is so in *Tetracladium Marchalianum*, *Articulospora tetracladia*, *Alatospora acuminata*, *Heliscus longibrachiatus*, *Tetrachaetum elegans* and *Clavariopsis aquatica*. Only in *Lemonniera aquatica* and in *Triscelophorus monosporus* is the conidium attached to its conidiophore near the point of divergence of the four arms of the spore.

In *Triscelophorus monosporus* the conidiophore is unbranched. In *Lemonniera aquatica* the conidiophore is usually branched to form a terminal group of several phialides, although, not infrequently, simple conidiophores are to be seen terminated by a single phialide, and with such *Triscelophorus monosporus* shows a very marked similarity. Again in *Triscelophorus monosporus* the four arms of the spore arise in succession but in *Lemonniera aquatica* they arise simultaneously and develop simultaneously. However, the most emphatic difference, which seems to make the inclusion of the two species in the same genus impossible, is that in *Triscelophorus monosporus* the spore is an aleuriospore whilst in *Lemonniera aquatica* it is a phialospore. The importance of this distinction in aquatic Hyphomycetes has already been discussed (Ingold, 1942).

Considering aquatic Hyphomycetes which produce aleuriospores, *Triscelophorus* appears to approach most nearly to *Dendrospora erecta* (Ingold, 1943). In that fungus the conidium has a long main axis with usually two or three whorls of lateral branches arising near its base, and the lowermost of these laterals may themselves branch. In *Dendrospora erecta* the number of branches in the whorl is usually three, especially in the basal whorl. If one imagined a spore of *Dendrospora erecta* with all except the bottom whorl of branches suppressed and with no tertiary ramuli, then a spore of much the same structure as that of *Triscelophorus monosporus* would result. However, it is not suggested that the two species could be included in the genus *Dendrospora*. A new genus *Triscelophorus* (τρι, three; σκέλος, leg; φερο, to bear) is proposed, the name being suggested by the spore which consists of a main axis bearing three basal branches (legs).

Triscelophorus n.gen.

Submerged aquatic fungi with branched septate mycelium. Conidia (aleuriospores) terminal, branched, consisting of: (1) an elongated main axis continuous with the conidiophore, and (2) elongated secondary ramuli forming a whorl of three branches arising from the lower part of the main axis.

Triscelophorus gen.nov.

Fungi aquatici submersi mycelio repente septato, ramoso. Conidia (aleuriosporae) acrogena, ramosa; ramus principalis elongatus, cum conidiophoro continuus; ramuli secundarii elongati, 3-verticillati ex inferiore parte rami principalis orientes.

Triscelophorus monosporus n.sp.

Submerged aquatic fungus with branched, septate mycelium. Conidiophore hyaline, simple, straight, 15–45 μ long, 1·5 μ broad, producing a single terminal conidium. Conidia (aleuriospores) hyaline, branched, aseptate (or with a single septum in the main axis just above the point of origin of the lateral branches); main axis continuous with the conidiophore, 50–70 μ long, 4–5 μ broad (at a distance of 3–5 μ from the base) tapering to 1·5 μ at the apex and to 1·5 μ at the truncate base; secondary ramuli in a whorl of three, arising at a distance of 3–5 μ from the base of the main axis, 40–50 μ long, 2·0–2·5 μ broad near the base tapering to 1·5 μ at the apex, base abruptly constricted to 1 μ.

On a submerged decaying leaf from the River Loddon near Reading, England.

Triscelophorus monosporus sp.nov.

Fungus aquaticus submersus mycelio repente septato, ramoso. Conidiophora hyalina, simplicia, erecta, 15–45 μ longa, 1·5 μ lata, unum modo conidium acrogenum gerentia. Conidia (aleuriosporae) hyalina, ramosa, aseptata, vel rami principalis basim versus uniseptata; axis princeps cum conidiophoro continuus, 50–70 μ longus, 3–5 μ supra basim 4–5 μ latus, apicem versus ad 1·5 μ sensim attenuatus, basi truncata 1·5 μ; ramuli secundarii 3-verticillati, circa 3–5 μ supra axis principalis basim orientes, 40–50 μ longi, deorsum 2·0–2·5 μ lati, basi subito ad 1 μ constricti, sursum ad 1·5 μ sensim attenuati. *Hab.*: in folio putrescente in flumine jacente ad Reading, Anglia. *Obs.*: a *Lemonniera* De Wild. conidiorum ortus modo (aleuriospora vice phialosporae) differt.

My best thanks are due to Miss E. M. Wakefield for her assistance with the Latin diagnosis.

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EXPLANATION OF PLATE VIII

Triscelophorus monosporus

All the photographs are from living material. The arrows indicate the junction of the conidium with the conidiophore.

Fig. 1. Conidiophore with nearly ripe conidium. The main axis of the spore and the lateral on the left are in focus, but the two laterals on the right are out of focus. × 600.

Figs. 2, 3. Spore primordium. From the lower cell of the primordium the first lateral branch of the spore is just beginning to form. Fig. 2, × 800; Fig. 3, × 760.

Fig. 4. Developing conidium. Two of the lateral arms of the spore have begun to develop; that on the left is in focus; the second arm is pointing directly towards the observer. × 900.

Fig. 5. Liberated spore. Note the characteristic truncate base of the main axis of the spore. × 590.

Fig. 6. Conidiophore with spore which is nearly mature. × 608.

(*Accepted for publication* 11 *January*, 1943)

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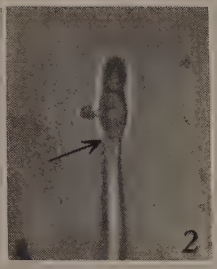
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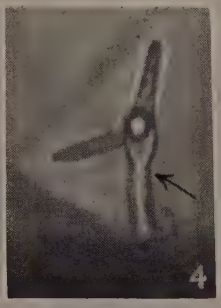
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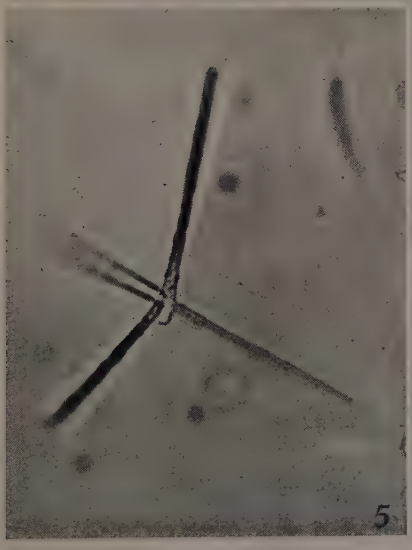
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THE OCCURRENCE OF *BOTRYTIS* SPP. ON ONION LEAVES WITH SPECIAL REFERENCE TO *B. SQUAMOSA*

By C. J. HICKMAN, *Research Officer, Agricultural Research Council (now at Long Ashton Field Laboratory)*
and D. ASHWORTH, *Royal Horticultural Society's Laboratory, Wisley*

(With Plate IX and 1 Text-figure)

At the beginning of October 1941 our attention was directed to a *Botrytis* die-back of onion leaves which was damaging crops of salad and bulbing varieties sown in the summer for overwintering. Typically affected leaves (Pl. IX, fig. 1) showed a pendent, withered terminal portion of varying length, greyish green or lighter in colour, frequently studded with elliptical or circular pale spots. At the junction of the withered portion with the remaining part of the leaf the tissues were water-soaked, while below there were elliptical or circular, slightly sunken parchment-coloured spots, usually sharply delimited but sometimes with water-soaked margins. On slightly affected leaves spotting alone was apparent. Older leaves were more severely attacked than young ones.

The affected leaves bore a species of *Botrytis* with unusually large conidia. The sporulating branches of the conidiophores were much septate and gave a very characteristic corrugated appearance to the fungus especially after the conidia had fallen.

A similar disease of onions was originally recorded by Ogilvie and Mulligan (1932) where they refer to a small sclerotial *Botrytis* which proved to be highly pathogenic to onions, while in a more recent account (1941) by Ogilvie, *B. cinerea* is recorded as the causal organism. Yarwood (1938) demonstrated the association of *B. cinerea* with the disease. Comparing it with Chocolate Spot of beans he describes two types of injury, (1) oval, white or greyish sterile lesions, and (2), by the merging of similar lesions, the collapse and death of the leaves from the tip downwards.

The data collected by Ogilvie and Mulligan were kindly placed at the disposal of one of us, and they suggested that not one but two fungi were concerned. One possessed few, relatively large sclerotia and produced abundant spores measuring on malt-extract agar 9·0–14·4 × 6·5–10·1 μ, average 11·7 × 7·8 μ, characters agreeing with *B. cinerea*. The other species had many small sclerotia with a rather matted mycelium. Spores taken from a culture on leek leaf agar approximately three months old measured 14·4–22·0 × 11·2–15·5 μ, average 17·6 × 12·8 μ. Both fungi were pathogenic when inoculated into leaf incisions.

From October onwards the disease was under continual observation. Many of the leaves bore abundant conidiophores of *Botrytis*, particularly on their withered tips, while non-sporing specimens incubated overnight

in a moist atmosphere formed conidiophores profusely. A few conidiophores were observed on some of the parchment-coloured lesions. Other lesions however, remained sterile, as described by Yarwood.

The species of *Botrytis* present on affected leaves agreed in all respects with *B. squamosa*, found by Walker (1926) in America causing 'small sclerotial neck rot' of onion bulbs. This species is characterized by large conidia and by a curious 'accordion'-like degeneration of the sporulating branches of the conidiophores after the conidia have fallen—a useful diagnostic character and one which first gave a clue to the identity of the English fungus. The young conidiophores are white in mass and densely crowded. They are relatively short and stout, measuring 300–380 × 12–13 μ and become septate with maturity. With continued growth the conidiophores darken and become less compacted. After producing a crop of conidia the spore-bearing branches contract to form the characteristic accordion-like branches (Pl. IX, fig. 2). Later these fall away and the conidiophores proliferate to produce another set of branches and spores. This process may be repeated three or four times and the points at which spore-bearing branches are formed are marked in old conidiophores by slight projections (Pl. IX, fig. 3). Sometimes proliferation may also take place laterally at one of these points, thus forming a compound conidiophore.

The hyaline conidia are ovoid or, occasionally, somewhat heart-shaped and germinate by one or two germ tubes. Their relative size can be judged from Text-fig. 1, where conidia of *B. cinerea* and *B. Allii* are drawn to the same scale. The following table illustrates the close similarity in spore size of the American and English isolations.

Table 1

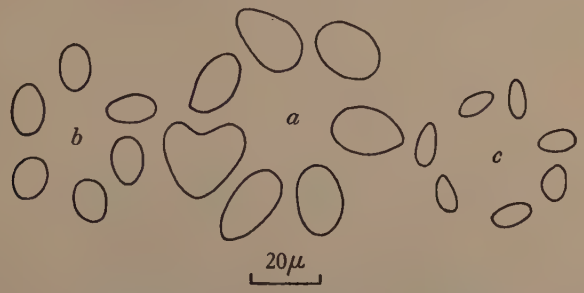
Source of culture	Range μ	Majority μ	Average μ	Medium
Walker	13–24 by 9–18	15–22 by 11–15	—	?
Hampton 1	16–25 by 9–20	19–22 by 13–16	20·9 by 14·7	Host
	13–24 by 9–16	16–20 by 12	18·5 by 12·6	*P.D. agar
Hampton 2	13–28 by 12–19	19–22 by 13–16	20·1 by 14·7	Host
	12–22 by 8–16	16–20 by 12–14	17·8 by 12·6	P.D. agar
Bretforton 1	14–24 by 11–19	19–22 by 13–16	19·4 by 15·2	Host
	12–26 by 10–18	16–22 by 10–12	19·1 by 11·7	P.D. agar
Bretforton 2	8–25 by 8–16	13–22 by 13	17·6 by 12·5	Host
	12–24 by 10–16	20 by 12–14	19·2 by 12·6	P.D. agar
Bretforton 3	12–26 by 12–18	16–20 by 12–14	19·5 by 13·4	Host
Pebworth	12–28 by 12–16	20–24 by 12–14	21·9 by 13·7	Host
	12–24 by 10–16	16–20 by 12–14	18·4 by 12·6	P.D. agar
Badsey 1	12–24 by 10–16	16–20 by 12–14	18·5 by 13·0	Host
Badsey 2	12–28 by 12–20	16–22 by 14–16	19·2 by 15·4	Host
Perdiswell	8–26 by 8–16	16–22 by 12–14	19·1 by 12·6	Host
Wisley	16–26 by 14–22	18–24 by 16–20	22·0 by 17·0	Host
			17·2 by 13·2	P.D. agar

* Potato-dextrose agar.

In a collection which was left in a moist chamber for several weeks, small black sclerotia, up to 5 mm. across, were observed on the leaves

which by this time were completely rotten and disorganized. Sclerotia were not found on diseased leaves in the field.

The fungus grows well on potato-dextrose agar, producing in slant cultures a white surface felt of mycelium which later becomes somewhat



Text-fig. 1. Showing the relative shape and size of conidia of *a*, *B. squamosa*; *b*, *B. cinerea*; *c*, *B. Allii*.

wavy, and, after three to four weeks at laboratory temperature, numerous black sclerotia 1–5 mm. across, often coalescing at the side of the culture. Conidia are rarely developed until cultures are about three months old, the conidiophores being borne almost exclusively on the surface of the sclerotia. In general, conidia produced in culture are slightly smaller than those on the host.

Recalling the description of the unidentified small sclerotial *Botrytis* isolated by Ogilvie and Mulligan, it will be observed that it agrees with *B. squamosa*—matted mycelium, numerous small sclerotia and large spore size. Further, the fact that spore measurements were taken from an old culture suggests the tardy conidial development of *B. squamosa*. It is therefore probable that this fungus was isolated as early as 1931 in this country.

In addition to *B. squamosa*, isolations corresponding to *B. cinerea* and of a third, at present unidentified, *Botrytis* were obtained from diseased onion foliage, suggesting that the disease is not associated with a single specific organism. In these investigations however, *B. squamosa* was the predominant fungus. It was recorded on ten occasions, from widely separated localities, while *B. cinerea* appeared only twice, once in association with *B. squamosa*.

As no healthy controls were available, no data could be gathered on the ultimate effect of the disease. In the spring, affected plants grew away from the disease apparently unharmed. The only exception was a variety imported from Egypt—Chandawil Bright—which was very susceptible both to *Botrytis* and to winter weather. The foliage was first almost totally destroyed in early October by *Botrytis*, and the destruction of the plants was completed by winter frosts. Apart from this variety, no marked varietal differences in susceptibility were observed, the popular White Lisbon salad onion and various bottoming varieties being equally affected.

No experiments were carried out to test the pathogenicity of the fungi isolated under controlled conditions. With the exception of Ogilvie's un-

published record that *B. cinerea* and what we conclude to be *B. squamosa* were pathogenic when agar-bearing mycelium was placed on wounded leaves, no information on this point exists in this country. According to an abstract in the *Review of Applied Mycology* of a paper by Van Poeteren (1939), *B. squamosa* was isolated from the dead leaves of potted onion plants but its connexion with the decay could not be determined. In America however, Walker (1926) tested the pathogenicity of this fungus towards onion foliage by spraying leaves with a spore suspension. After finding that leaves were not attacked unless plants were left in a moist chamber for a week or more (at 18° C.), he remarks that 'in an extremely humid environment having a favourable temperature, infection of the aerial parts by *B. squamosa* may occur', but that 'there is little evidence that this form causes a destructive leaf blight'. He presents no evidence of leaf infection by this fungus in the field during the growing season of the bulb onion crop. Similarly, *Botrytis* infection did not appear here on onion foliage during the summer months, its development being limited to the autumn and winter period. One further point of significance regarding the etiology of this disease is that *Botrytis* infection was sometimes associated with mild attack by Downy Mildew (*Peronospora Schleideniana*). The conidiophores of the latter fungus were sparsely distributed amongst the dense masses of *Botrytis* fructifications. It seems probable that we are dealing here with an example of facultative parasitism, infection being governed either by increased susceptibility of the host during autumn and winter as a result of adverse weather conditions, Downy Mildew attack and/or by the favourable effect of the relatively moist conditions, on the development of *Botrytis*.

The occurrence of *B. squamosa* is of some importance because it may cause a neck rot of onion bulbs (Walker, 1926). It does not seem to be virulently parasitic however, for when pieces of an agar culture of the fungus were laid on the necks of onion bulbs in a moist chamber no rotting followed. We have not found it naturally occurring on onion bulbs but this may only reflect its rarity as an agent of onion neck rot, for Walker himself found it to be less common than the other neck-rot organisms *B. Allii* and *B. byssoidea*.

Summary

A die-back disease of onion foliage characterized by pale spotting and death of the leaves from the tip downwards, associated with *Botrytis* infection, was investigated during 1941–2. Of three species of *Botrytis* isolated from diseased leaves, *B. squamosa*, recorded for the first time in this country, was the predominant organism. The other fungi were *B. cinerea* and an unidentified form. Infection was limited to autumn and winter and plants usually grew away healthy in spring and summer. The disease is probably an example of facultative parasitism.

We wish to express our gratitude to Mr L. Ogilvie for permission to include certain data and to Dr C. G. C. Chesters for assistance in taking photographs. Our acknowledgments are also due to Long Ashton Research Station for Pl. IX, fig. 1.

Fig. 1

Fig. 2

Fig. 3

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EXPLANATION OF PLATE IX

Fig. 1. White Lisbon Onion leaves affected by *Botrytis* die-back. Approx. half natural size.
Fig. 2. Conidiophores of *B. squamosa* showing the 'accordion' degeneration of the spore-bearing branches after the conidia have fallen. ×600.
Fig. 3. Old conidiophores of *B. squamosa* showing the points of attachment of former spore-bearing branches. ×85.

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OBSERVATIONS ON THE GENUS *MYROTHECIUM* TODE

I. THE THREE CLASSIC SPECIES

By N. C. PRESTON

(With Plates X and XI and 7 Text-figures)

Introduction

My attention was drawn to this genus when a *Myrothecium* tentatively referred to *M. roridum* Tode was found to be an active parasite of cultivated violas (Preston, 1934). It was also recorded as parasitic on *Antirrhinum majus* by Taubenhaus (1934) in U.S.A. and in 1939 it was found at Cambridge on the same host by Brooks who sent it to me. An attempt to establish the identity of the fungus in *Viola* led to a general study of the genus and primarily to an examination of the three classic species considered here.

Historical

The genus *Myrothecium*, now classified in the Tuberculariaceae, was founded by Tode (1790) and was adopted in an emended form by Fries (*Systema Mycologicum* 1829) with four species, three of which he distinguished according to the nature of the disk and the shape of the spores thus:

M. roridum Tode: disk swollen, spores cylindric.

M. verrucaria (Alb. & Schwein.) Ditmar: disk flattened, spores ovate.

M. inundatum Tode: disk flat, spores globose.

The fourth species, *M. scybalorum* (Schum.) Fr., is otherwise only known from Schumacher's (1803) description and figure as *Peziza scybalorum*.

A search of the available *exsiccata* showed that the three classical species recognized by Fries can be clearly distinguished, though certain modifications of the original diagnoses must be made. During this study two of these species, *M. roridum* and *M. verrucaria*, have also been recognized in living material obtained from widely separated localities, and cultures of them have been maintained and studied.

The original diagnosis for the genus (Tode, 1790) was: '*Fungus cyathiformis*; *cupula superni volvata*; *repletura seminali lentoviscida*', i.e. Fungus cup-shaped; cups surrounded by a sheath; when filled with spores slowly sticky. Tode described five species: *M. roridum*, *M. inundatum*, and three others which were later stated by Fries to belong to quite other genera. He did not describe or figure the spores. The habitat of *M. roridum* was given as the damp remains of oak and pine branches; that of *M. inundatum* as a dried up agaric. Tode's genus was emended by Link (1809) who based his description on *M. inundatum* Tode and stated that Tode's other species

were very different. His diagnosis was as follows: '*Sporangium figurae indeterminatae. Peridium simplex laxe floccosum tandem in medio evanescens. Sporidia minutissima globosa, prima aetate fluidiuscula, dein compacta*', i.e. Sporangium irregular in shape. Peridium simple, loosely woolly, at length disappearing at the centre. Spores very small, globose, at first somewhat fluid, then compact. Meanwhile, Albertini and Schweinitz (1805) had described a fungus said to be frequently found on very rotten cucumber leaves in Germany. This they named *Peziza verrucaria*, although they recognized its resemblance to the *Myrothecia* of Tode as the disk of the receptacle was at first adhesively sticky and then hardened; they did not describe its spores.

Ditmar (1813) described and figured *M. inundatum*, repeating Link's statement that the spores were globose. He also collected a fungus with oval spores on *Lapsana communis* and identified it with *Peziza verrucaria* A. & S. which he transferred as *Myrothecium verrucaria* (A. & S.) Ditmar. It was Tode's genus as emended by Link and Ditmar which Fries (1829) accepted. The characteristic feature of the genus, which evidently impressed Tode and is specifically referred to by both Schumacher (1803) and Link (1809), is the semi-liquid or viscid nature of the spore mass when fresh. Three other points in Link's and Ditmar's emendation require particular attention. First, Link included only a single species, *M. inundatum*, in his emended genus; second, both Link (1809) and Ditmar (1813) described its spores as globose; and third, the reference to a woolly (*laxe floccosum*) margin to the disk.

Myrothecium was first recorded for Britain by Greville (1825) when he described *M. Carmichaelii* occurring on 'masses of subputrescent vegetable substances' in Appin. He stated that this species was readily distinguishable from both *M. inundatum* and *M. verrucaria* in its cylindrical spores. Fries (1829) identified Greville's new species with *M. roridum* Tode, which was thus reinstated in the genus.

No more exact information about these three species became available until Saccardo (1880) identified *M. roridum* and *M. verrucaria*, and, in 1881, figured and described them and *M. inundatum*. His descriptions are as follows: '*M. roridum sporodochia plana, atra, albo-marginata, conidia, cylindrica, utrinque obtusa* 8–10 × 2 μ (raro 14 × 2 μ), 2 *guttulata, dilute olivacea, basidiis filiformibus* 30 × 2 μ *suffulta*' and '*M. verrucaria* differt in *conidiis oblongo-ovatis* 9 × 3 μ, 2 *guttulatis, olivaceis, basidiis filiformibus sesquilongioribus suffultis*', i.e. *M. roridum* sporodochia flat, black, white fringed, conidia cylindrical with blunt ends 8–10 × 2 μ (rarely 14 × 2 μ), biguttulate, pale olivaceous, supported on filiform basidia 30 × 2 μ, and *M. verrucaria* differs in (having) conidia oblong-ovate 9 × 3 μ, biguttulate, olivaceous supported on filiform basidia about half as long again as the spores. His figure of *M. inundatum* shows that he regarded the spores of this species as semi-globular, measuring 3–4 × 1·5 μ.

Höhnel (1905) pronounced the spores of *M. inundatum* to be oblong rod-shaped, 3–4 × 1–1·5 μ, and not globose. He also stated that he found long white setae in young specimens of this species though they were generally absent from the mature margin of the sporodochium.

The type species

As we have seen, only one of Fries's three clearly defined species, *M. inundatum*, was actually included by Link and Ditmar in their emended genus which Fries accepted. As this species alone has remained in the genus since its inception it is proposed as its natural type. Link no doubt identified the species from its peculiar habitat, viz. dried agarics, and, since it is

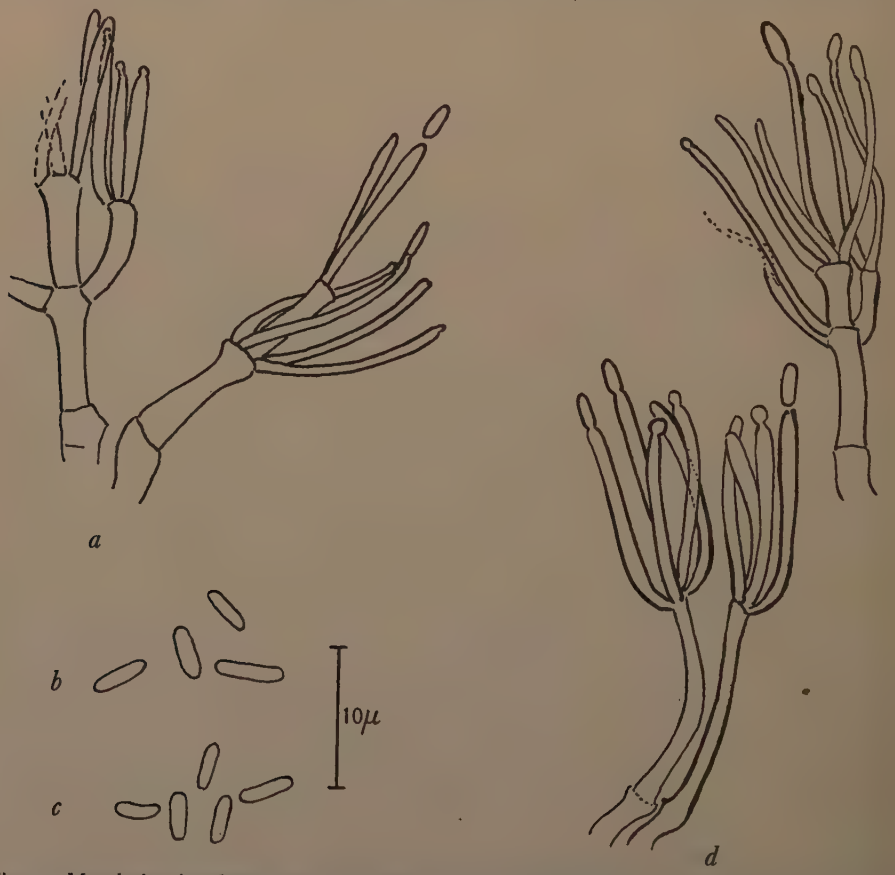

Fig. 1. *Myrothecium inundatum* Tode. *a*, conidiophores and phialides ex Carmichael Herb. Hort. Edinb. (freehand drawing). Spores: *b*, ex Carmichael Herb. Kew; *c*, ex Herb. Petch (on *Russula adusta*). *d*, ex Ellis and Everhart Herb. Kew (freehand drawing). *a*, ×2000 approx.; *b*, *c*, ×1800; *d*, ×2000 approx.

almost certain that no type specimen now exists, it seems legitimate to assume that the published exsiccata of *M. inundatum*, all of which are on similar substrata, do indeed represent the same species as that originally described by Tode. This being so, it is evident that Link's description of the spores as globose is incorrect. All the specimens examined bear out Höhnel's statement that they are rod-like, 3–4 × 1–1·5 μ (Text-fig. 1), but

since short rods may easily appear to be spherical, especially under a low magnification, Link's error is readily understandable. The presence of long white setae, figured by Nees (1817) and described by Höhnel, has also been confirmed. Though these could not be found in the Kew exsiccata they were easily recognizable in most of the fructifications of more recently collected material which Mr T. Petch generously provided from his own herbarium (Pl. X).

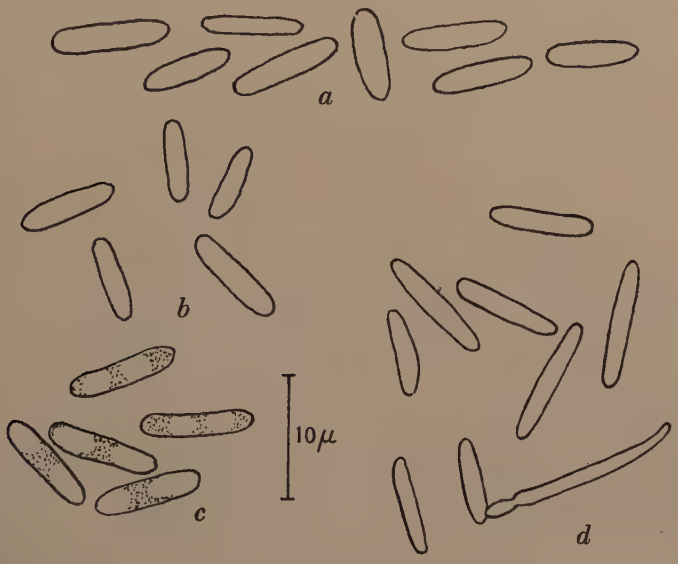

Fig. 2. *Myrothecium roridum* Tode ex Fr. Spores. *a*, ex Antirrhinum; *b*, ex *Viola*; *c*, ex *Lycopersicum*; and *d*, *M. Carmichaelii* Grev. ex Type specimen Herb. Hort. Edinb.

The other classic species

The original diagnosis (Greville, 1825) for *M. Carmichaelii* Grev. is: '*Peridio polymorpho candido; sporulis viridibus nigrescentibus cylindricis*', i.e. peridium irregular in form, white; with sporules green becoming black, cylindrical. The type specimen of *M. Carmichaelii* Grev., still preserved in the Edinburgh Herbarium, has been examined. Its fructifications conform to Tode's original description of *M. roridum*. Fries regarded *M. Carmichaelii* Grev. as synonymous with *M. roridum* Tode. Following Fries, therefore, we can make use of the type of *M. Carmichaelii* for the recognition of *M. roridum* Tode as accepted since the time of Fries. The parasite on *Viola* can thus be identified as *M. roridum* Tode in the accepted sense, and a number of similar fungi received from the Imperial Mycological Institute can also be referred to this species; these will be dealt with later.

The third species accepted by Fries, *M. verrucaria* (Alb. & Schwein.) Ditm., is readily distinguishable by the shape of the spores, described as ovate (Fries), or oblong-ovate (Saccardo). Whether the type specimen of *Peziza verrucaria* A. & S. still exists is doubtful, and, as it has apparently

never been re-examined, we have no means of verifying the shape of its spores. The three published exsiccata issued as *M. verrucaria* A. & S., in the Kew Herbarium, all have distinctly oval spores quite different in shape from, and somewhat darker in colour than those of *M. roridum*. Their dimensions are slightly smaller than those given by Saccardo, but in shape they conform to his figure (Pl. III). When highly magnified, the spores of all three specimens show a distinct flattening, or even a minute protuberance, at the broader (basal) end and they are therefore correctly described as truncate. Three living specimens of a similar fungus obtained in cultures from the Imperial Mycological Institute have spores corresponding closely both in shape and size with those of the Kew exsiccata of *M. verrucaria* and they are therefore referred to this species (Text-fig. 3*a*, *b*).

Fig. 3*a*. *Myrothecium verrucaria* Tode ex Fr. ex Citrus fruits (Bates) (freehand drawing).

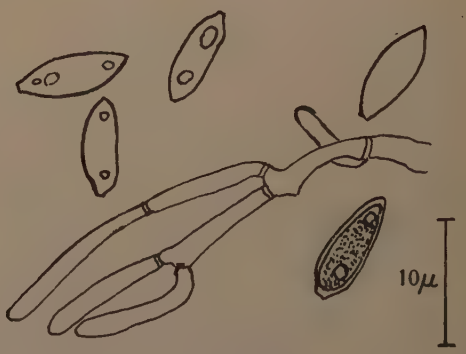

Fig. 3*b*. *Myrothecium verrucaria* Tode ex Fr. ex Potato (Cyprus) Nattrass.

While it has been found possible to distinguish the three species of *Myrothecium*, viz. *M. inundatum*, *M. roridum* and *M. verrucaria*, by means of spore shape and size, it is very doubtful whether Fries's other criterion for their separation, the shape of the disk, is tenable as a specific character. If by the term 'disk' Fries meant the shape of the spore-mass, this of course varies with the age and consequent dryness of the fructifications. In young viscid fructifications of both the *roridum* and the *verrucaria* types, the spore-mass is generally rounded or conical, but after drying it tends to become flat. The dried specimens of *M. inundatum* which have been examined have flat or even slightly concave spore-masses, but the spores of this species are undoubtedly cylindrical though much smaller than those of what we may call the *roridum* type. Supposing, alternatively, that when describing the 'disk' Fries is referring to the hymenial surface formed by the closely aggregated phialides directly below the spore-mass itself, this still provides no distinguishing character corresponding with the shape of the spores. In both cylindrical-spored or truncate-spored forms this disk may be either flat, umbonate (swollen) or even undulating.

The living material

(1) *Myrothecium roridum.* Living British material (Text-figs. 2, 4 and 5) of this species has been obtained from three different host plants all of which are cultivated species, viz. *Viola tricolor*, *Antirrhinum majus* and *Lycopersicum esculentum.* I have not collected it upon any wild species of *Viola* or other plants nor upon plant debris. It occurs quite frequently upon garden violas, and isolates have been obtained from a number of different varieties of these. The isolate from *Antirrhinum* was kindly supplied by Prof. Brooks from Cambridge, and this was also found to grow readily upon detached but unsterilized *Viola* stems. The material from tomato was isolated from a sporodochium occurring upon a greenhouse plant, the

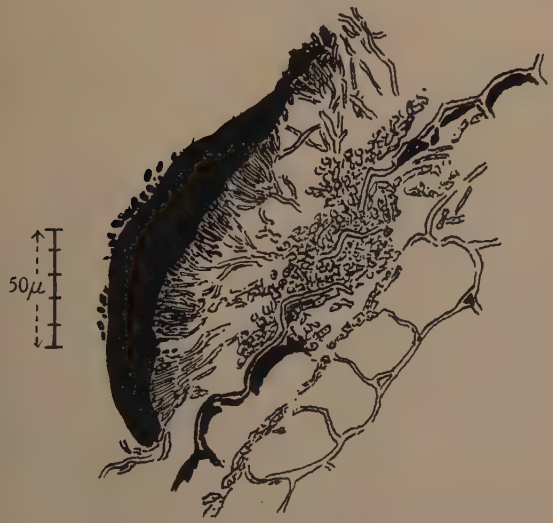

Fig. 4. *Myrothecium roridum* Tode ex Fr. Section through sporodochium on *Viola* (natural infection).

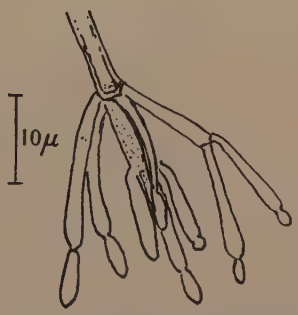

Fig. 5. *Myrothecium roridum* Tode ex Fr. ex *Antirrhinum majus.*

stem of which had been attacked also by *Botrytis cinerea.* Inoculation of this isolate on to young living tomato plants produced only very slight superficial lesions and no sporodochia were formed.

The isolates obtained from these three plants have been grown upon a variety of artificial media such as cherry, malt extract, corn-meal and potato-dextrose agars and they produce sporodochia upon all of them. On corn-meal agar mycelial development is slight and the fungus from *Viola* usually stains this medium bright yellow. Apart from this colour reaction, the isolates are indistinguishable from one another both in their macroscopic appearance and in the shape and dimensions of their spores (Text-fig. 2). They closely resemble the exsiccata of *M. roridum* Tode, including the type specimen of *M. Carmichaelii* Grev., though their spores are somewhat shorter and broader, on the average, than those of the herbarium specimens. The spore and phialid measurements are compared in Table 1.

In addition to the British material just described several cultures of *Myrothecium* from the Imperial Mycological Institute have been critically examined. Among these, the following, all collected by Deighton in Sierra Leone, are considered referable to *Myrothecium roridum* Tode ex Fr.:

No. 937, ex *Hibiscus esculentus*.
No. 880, ex *Dolichos Lablab*.
No. C. B. 881 A, also ex *Dolichos Lablab*. (Text-fig. 6).
No. 849 A, ex *Trichosanthes*.
An unnumbered specimen, ex *Asclepias* sp.

Table 1. *Spore measurements of* Myrothecium roridum *Tode ex Fr. from various sources*

Source	Spores: Range μ	Spores: Average μ
Exsiccata:		
M. Carmichaelii Grev., Appin Type, Herb. Hort. Edin.	8–10 × 1–2	9·5 × 1·3
M. roridum Tode, H. W. R(avenal) Herb. Kew, North America	8–12 × 2–2·5	9·0 × 2·0
Isolates:		
ex *Viola*, England	5·5–8·0 × 1·5–2·5	6·6 × 1·9
ex *Antirrhinum*, England	6·0–9·0 × 1·5–2·5	7·1 × 1·9
ex *Lycopersicum*, England	6·0–10·0 × 1·5–2·5	8·3 × 2·0
ex *Hibiscus*, West Africa	6·5–10·5 × 1·5–2·5	9·4 × 2·0
ex *Dolichos*, West Africa	6·0–11·0 × 2·0–3·0	8·3 × 2·6
ex *Trichosanthes*, West Africa	5·5–9·0 × 2·0	7·4 × 2·0
ex *Asclepias*, West Africa	6·0–8·0 × 1·0–2·0	6·9 × 1·7

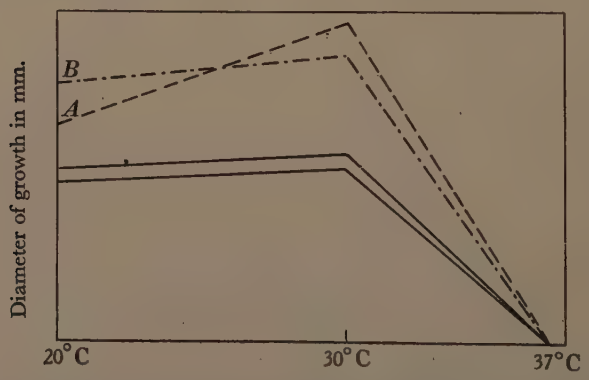

Fig. 6. Extent of growth of *M. roridum* at different temperatures after 4 days. Continuous lines = British isolates, both from *Viola*; broken lines = West African isolates. *A*, from *Asclepias*; *B*, from *Dolichos Lablab*.

Of these three fungi Nos. 937 and 880 reacted as very active parasites when inoculated on to living *Viola* stems, producing typical lesions upon which sporodochia developed after a few days. The fungus No. 849 A, ex *Trichosanthes*, differs somewhat from the others in producing, on agar, a coarse mycelium which tends to form into thick strands, but its sporodochia and spores are typical. This fungus either failed to infect, or produced only very slight lesions, when inoculated on to living *Violas*.

Temperature and pH relations. In spite of the difference in their habitat both the British and African specimens of *M. roridum* showed a very similar response to temperature in their rate of growth. The optimum temperature for each is about 30° C., but all grow almost equally well at 20° C., the African forms making slightly more rapid growth than the British ones at either of these temperatures (Text-fig. 6). Growth was inhibited in all at a temperature of 37° C.; the African forms, however, remained viable after four days at this temperature and resumed growth when transferred to a temperature of 23° C., whilst the British forms made no recovery under similar conditions (Text-fig. 6).

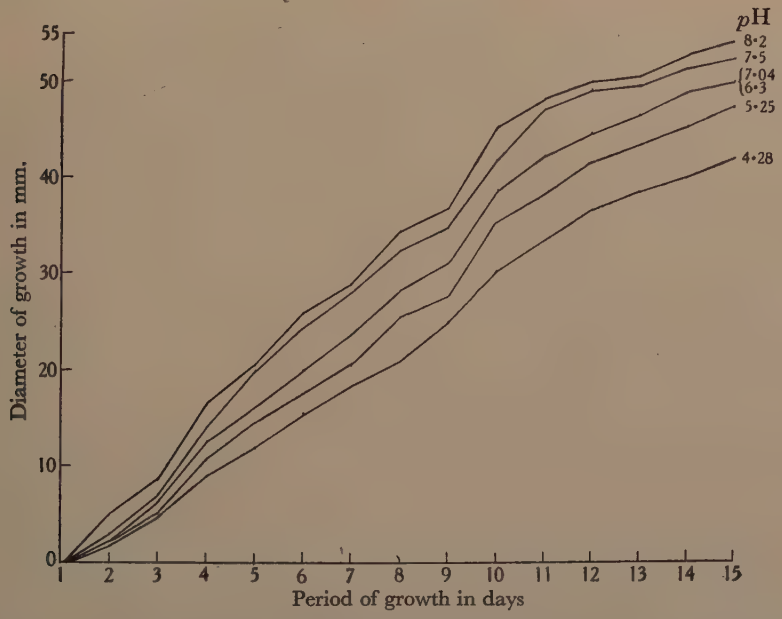

Fig. 7. Effect of *p*H of medium on rate of growth of *Myrothecium roridum*, isolated from *Viola*. Each reading = average of three Petri-dish cultures. Medium: 2·5% malt extract agar adjusted for *p*H. [The curves for *p*H values 7·04 and 6·3 became identical after 7 days and closely approximated one another up to this date; a mean reading is therefore given for these over the first 7 days.]

The effect of the *p*H of the medium has been investigated only for the British isolates from *Viola*. These were grown on 2·5% malt extract adjusted in range from *p*H 3·4 to 8·2. No growth occurred on the very acid medium, but the fungus grew normally at *p*H 4·8 and the rate of growth increased slightly with rise of *p*H from this point to the maximum of 8·2. Alkalinity of the medium was definitely favourable to growth as will be seen by reference to the graph (Text-fig. 7). The figures for each *p*H are the average of the extent of growth measured on three plate cultures. The plates were inoculated by puncturing the agar at the centre with a platinum wire previously dipped in a suspension of the requisite spores in sterile water.

(2) *Myrothecium verrucaria.* This species is easily distinguishable from

M. roridum by its elliptical, ovoid or lemon-shaped spores though the sporodochia are very similar. It appears to be unrecorded in Britain.

Three living cultures, referred to *M. verrucaria* A. & S., after comparison with the published exsiccata of the species, were obtained from the Imperial Mycological Institute. These are:

No. 162. Collected by G. R. Bates from the washings of citrus fruits in Southern Rhodesia.

No. 878. Collected by R. M. Nattrass from potato foliage in Cyprus.

A culture (unnumbered) isolated from soil in the Sudan by T. W. Clouston.

Nattrass's fungus is evidently a parasitic form. It was originally obtained from living potato haulms and has been found to grow quite readily on detached but living pieces of potato haulm and also upon living cucumber leaves on moist filter paper in large deep Petri dishes. This is of interest since Albertini and Schweinitz described their *M. verrucaria* as being frequently found upon subputrescent cucumber leaves and it seems that this species, like *M. roridum*, has formerly been regarded only as a saprophyte.

Temperature relations. The optimum temperature for growth of the isolates from potato and citrus is about 30° C. but, unlike *M. roridum*, *M. verrucaria* can tolerate a temperature of 37° C. though at this temperature its growth is retarded and tends to become abnormal and wrinkled.

All three isolates grow and fructify readily upon the same artificial media as were used for the culture of *M. roridum*.

(3) *Other species of* Myrothecium. Two other species received from the Imperial Mycological Institute will be described more fully in another paper. One of these, No. 145, collected by Jollyman in Nyassaland on drying tobacco leaves, is possibly identical with *M. gramineum* Lib. It has rod-like spores similar to those of *M. roridum*, but its rather large sporodochia are provided with long pointed setae.

The other fungus, isolated by Neil from a clay soil in New Zealand, appears to be a new species. It is distinguished by having distinctly striate spores.

The following are emended descriptions of the genus *Myrothecium* and of its three classic species.

Myrothecium Tode ex Fr.

Sporodochia shallow cups, with or without a pseudoparenchymatous base, covered with a viscid spore-mass at first green, becoming jet black, with a white margin of flocculent contorted hyphae, with or without setae. *Conidiophores* septate, hyaline or olivaceous, consisting of a main axis which is once or twice branched, and crowned with a whorl of closely appressed phialides. *Phialides* slenderly clavate, hyaline or pale olive green. *Conidia* small, cylindrical, or elliptical with a truncate base; continuous, subhyaline or pale olive green, abstricted singly to form a black viscid mass.

Myrothecium inundatum Tode ex Fr.

Sporodochia small 0·3 to about 1·5 mm. in diameter, about 0·05 mm. deep, circular or irregular in surface view, often confluent, black with pure white floccose margin and numerous evanescent setae. *Setae* arising more or less horizontally from below the sporodochium and bending sharply upwards at its margin, hyaline, thick-walled, septate, tapering with blunt apices, usually three to five celled, 100 to at least 300 μ long, 3–4 μ wide in region of basal septum, slightly narrower below and tapering to 2 μ at apex. *Conidiophores* erect, irregularly branched, hyaline; main axis tapering, three to four celled, cells slightly broadening below their distal septa; branches one to two celled arising immediately below a septum of the parent axis, closely intertwined. *Phialides* very slenderly clavate, hyaline, 9–22 μ long, 1–2 μ broad, arising in groups usually of from three to seven from the apices of the main axis and its branches or borne laterally, either singly or in small whorls, just below a septum of the parent branch; forming a compact hymenium-like layer. *Spores* very small, continuous, cylindrical with rounded ends, 3–4 $\mu \times$ 1–2 μ, sub-hyaline or greenish, aggregated when dry into a firm flat or slightly concave mass.

Myrothecium roridum Tode ex Fr.

Sporodochia sessile, discoid, circular or irregular in surface view, 0·1 to about 1·5 mm. in diameter, about 0·05–0·1 mm. deep, often confluent into larger masses; green at first, becoming black, white rimmed, without setae, arising either directly from the mycelium or from a pseudoparenchymatous stroma erupting from the epidermal cells of the host and composed of the intertwining conidiophores. Margin woolly consisting of loosely intertwined unicellular contorted hyphae with blunt ends arising from below the conidiophores and tending to curve inwards. *Conidiophores* erect, once or twice branched, septate, hyaline, main axis tapering, three to four celled, cells broadening slightly below their distal septa, basal cell about 30 $\times$ 3 μ, apical cell about 10 $\times$ 1·5 μ; branches one or two celled, arising singly or in pairs or whorls either directly from the terminal cell of the parent axis or immediately below the septum of an intermediate cell, each branch terminating in a whorl of phialides. *Phialides* slenderly clavate, straight, hyaline, usually arranged in whorls of three to seven at the apices of the main axis and its branches but sometimes arising singly or in small whorls immediately below a distal septum of an intermediate cell, 10–12 $\times$ 1–2 μ, forming a closely packed hymenium-like layer. *Conidia* cylindrical or very slightly tapering with rounded ends, continuous, two to three guttulate, hyaline at first, becoming pale green, 5–9 $\times$ 1–2·5 μ (average 8 $\times$ 2 μ). Spore-mass green, becoming jet black, viscid, globular or conical at first, finally dry, dull black, flattened or slightly concave.

Myrothecium verrucaria (Alb. & Schwein.) Ditmar ex Fr.

Sporodochia, conidiophores and phialides essentially similar to those of *Myrothecium roridum*. *Conidia* elliptical with a truncate base, smooth, continuous, two to three guttulate, subhyaline to pale olive green 6–10 $\times$ 2–4·5 μ. Spore-

mass green, becoming jet black, viscid, globular or conical at first, becoming dry, dull black and flattened.

I gratefully acknowledge the loan of the type specimen of *Myrothecium Carmichaelii* and other material from the Edinburgh Herbarium and the facilities afforded me at the Royal Herbarium, Kew, and the Imperial Mycological Institute. My thanks are also due to Dr C. G. Chesters for the reproduction of the plate from *Grevillea*, to Mr T. Petch and Prof. F. T. Brooks for material which they provided, and especially to Mr E. W. Mason for invaluable criticism and help throughout, particularly in connexion with the historical survey and the reproduction of plates.

Note. After the paper was written, Mr G. Smith (London School of Tropical Medicine) furnished me with what seems to be the first British record of *Myrothecium verrucaria*. The fungus was found by Dr Turfitt on an old canvas shoe (possibly of American origin) in Sherwood Forest.

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EXPLANATION OF PLATES X AND XI

Plate X

Fig. 1. *Myrothecium inundatum* after Ditmar (1813).
Fig. 2. *Myrothecium inundatum* after Saccardo (1881).
Fig. 3. *Myrothecium inundatum* (on *Russula adusta*) ex Herb. Petch. Sporodochium; spore-mass removed to expose setae, × 100.
Fig. 4. *Myrothecium inundatum* (on *Russula adusta*) ex Herb. Petch. Spores, × 1000.

Plate XI

Fig. 5. *Myrothecium roridum* after Saccardo (1881).
Fig. 6. *Myrothecium verrucaria* after Saccardo (1881).
Fig. 7. *Myrothecium Carmichaelii* after Greville (1825).
Fig. 8. *Myrothecium Carmichaelii* ex Herb. Hort. Edin. Phialides and spores, × 1000.
Fig. 9. *Myrothecium roridum* on *Viola*. Two sporodochia viewed from above, × 50 approx.

(*Accepted for publication* 20 *February* 1943)

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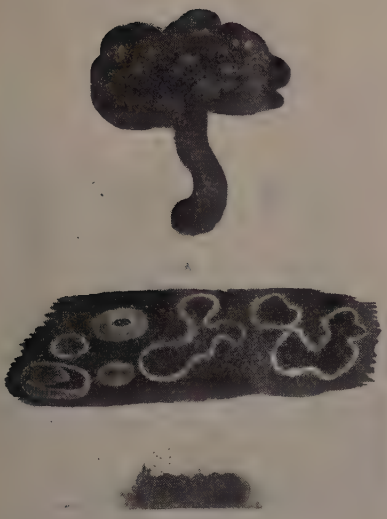

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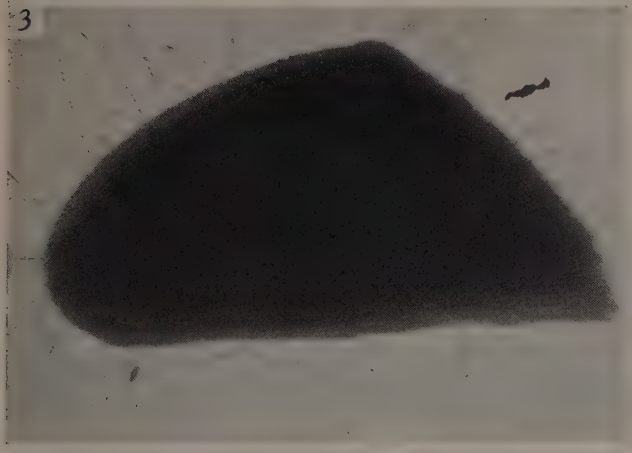

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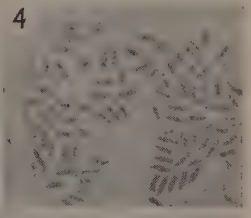

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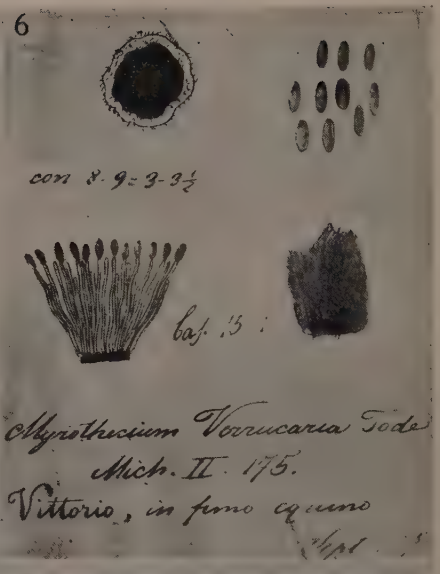
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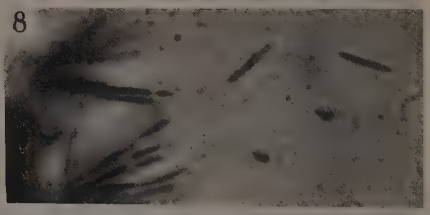
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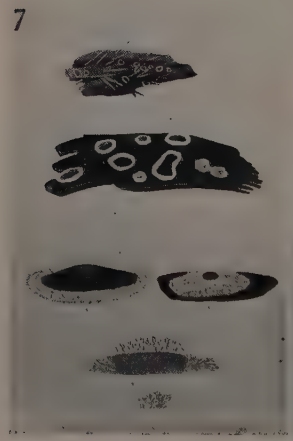
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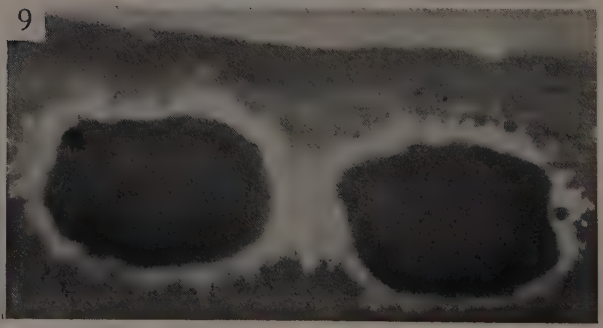
9

STUDIES IN THE GENUS *USTULINA* WITH SPECIAL REFERENCE TO PARASITISM

VI. A BRIEF ACCOUNT OF HEART ROT OF BEECH (*FAGUS SYLVATICA* L.) CAUSED BY *USTULINA*

By W. H. WILKINS, *Mycology Laboratory, University Department of Botany, Oxford*

(With Plate XII)

When starting the investigation into the pathogenicity of *Ustulina* in 1933, the intention was to show that beech is subject to a serious heart rot caused by this fungus. This work was delayed by inability to secure adequate evidence because material for detailed examination was not available. In the meantime, however, it has been shown that *Ustulina* causes a heart rot of lime (Wilkins, 1936) and of elm (Wilkins, 1939). In both trees no fungus other than *Ustulina* could be isolated from the diseased timber, so this was obviously the pathogen. Several beech trees have been examined during the past six years, and though no old tree has been found in which *Ustulina* was the only fungus present, it seems probable that it is often the primary and major cause of decay, for in younger trees, where decay is less advanced, no other causal organism has been isolated.

Recently, a beech tree which showed typical *Ustulina* heart rot was felled in the Botanic Gardens, Oxford. Though, owing to the author's preoccupation with medical research, this tree was not investigated in detail, it seems desirable briefly to put this and other cases of *Ustulina* heart rot of beech on record.

The tree was a fine specimen, about 170 years old with no external symptoms of disease. When cut across about 2 ft. 6 in. above ground level, the greater part of the centre of the trunk was seen to be decayed in the manner characteristic of *Ustulina* (Pl. XII, fig. 3). Isolations from the decayed timber showed that though certain other (unidentified) fungi were present, the greater part of the wood was diseased by *Ustulina* as most of the isolations gave pure cultures of that fungus. This tree was situated about twenty yards from the site of the lime tree previously recorded by me (1936) as being diseased by *Ustulina*. This might imply infection via lateral roots, but though the roots of the lime were to some extent decayed, this decay did not extend to the extremities, and, moreover, the lateral roots of the beech were quite sound. The centre of the root was completely rotten, and it seems probable that the heart-rot infection was due to die-back and consequent decay of the tap-root system as described by Day (1934). *Ustulina* may be a wound parasite, but in all the cases of heart rot of beech examined by me, and in most other heart rots caused by this fungus, infection was invariably via the decayed tap root. The decay extended up the trunk to a height of 12 ft., rendering the timber economically useless.

The symptoms of decay in this tree are almost identical with those found in beech trees examined at Blenheim Park, Woodstock (Pl. XII,

fig. 1), Arundel Park, Sussex (Pl. XII, fig. 2) and elsewhere, all of which were decayed by *Ustulina*. Macroscopic examination of a transverse section across a diseased trunk indicates the major symptoms of decay as follows:

(1) The centre of the trunk is more or less occupied by a patchily discoloured area with a very irregular outline which bears no relation to the distribution of annual rings (Pl. XII, figs. 1–3).

(2) This area may be bounded by a definite black line as shown on the left side of the section illustrated in Pl. XII, fig. 2. If this line is not present when the tree is freshly cut, it may develop as the timber dries out.

(3) If a transverse slice of the trunk be put in the dark and kept moist, the surface will probably become covered with the dark, felty, white-edged mycelium of *Ustulina* (Wilkins, 1936, Pl. XII, fig. 3).

(4) Certain isolated patches of the timber in the discoloured area are distinguished as being darker, softer and distinctly more wet than the rest. These patches usually indicate the presence of another species of fungus. Such patches are well shown in Pl. XII, figs. 1, 3.

(5) Whether a peripheral black line is evident or not, the most characteristic feature of the disease is the presence of black lines irregularly distributed throughout the decayed wood (Pl. XII, figs. 1, 4). These have a general tendency to run radially but with numerous interconnexions and irregularities. They may occasionally be double. Black lines may be produced by certain other fungi but those of *Ustulina* are very characteristic and slight experience enables them to be used as a diagnostic feature. An example of the general arrangement of the black lines in a dried-out block of timber is shown in Pl. XII, fig. 4. A photograph of a trunk of beech showing typical symptoms of *Ustulina* heart rot, with peripheral black line well emphasised in certain parts, is shown by Cartwright and Findlay (1942) Pl. V, fig. c.

It is hoped that microscopic examination of the fungus timber relationship may be done later.

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EXPLANATION OF PLATE XII

Transverse sections across beech trunks decayed by *Ustulina* heart rot.

Fig. 1. An advanced stage of decay in tree from Blenheim Park, Woodstock.

Fig. 2. A young beech from Arundel Park, Sussex, with actively growing *Ustulina*.

Fig. 3. Tree from Botanic Gardens, Oxford, with a stage of decay intermediate between the above two.

Fig. 4. Transverse section of dried-out timber from fig. 1 enlarged to show black line.

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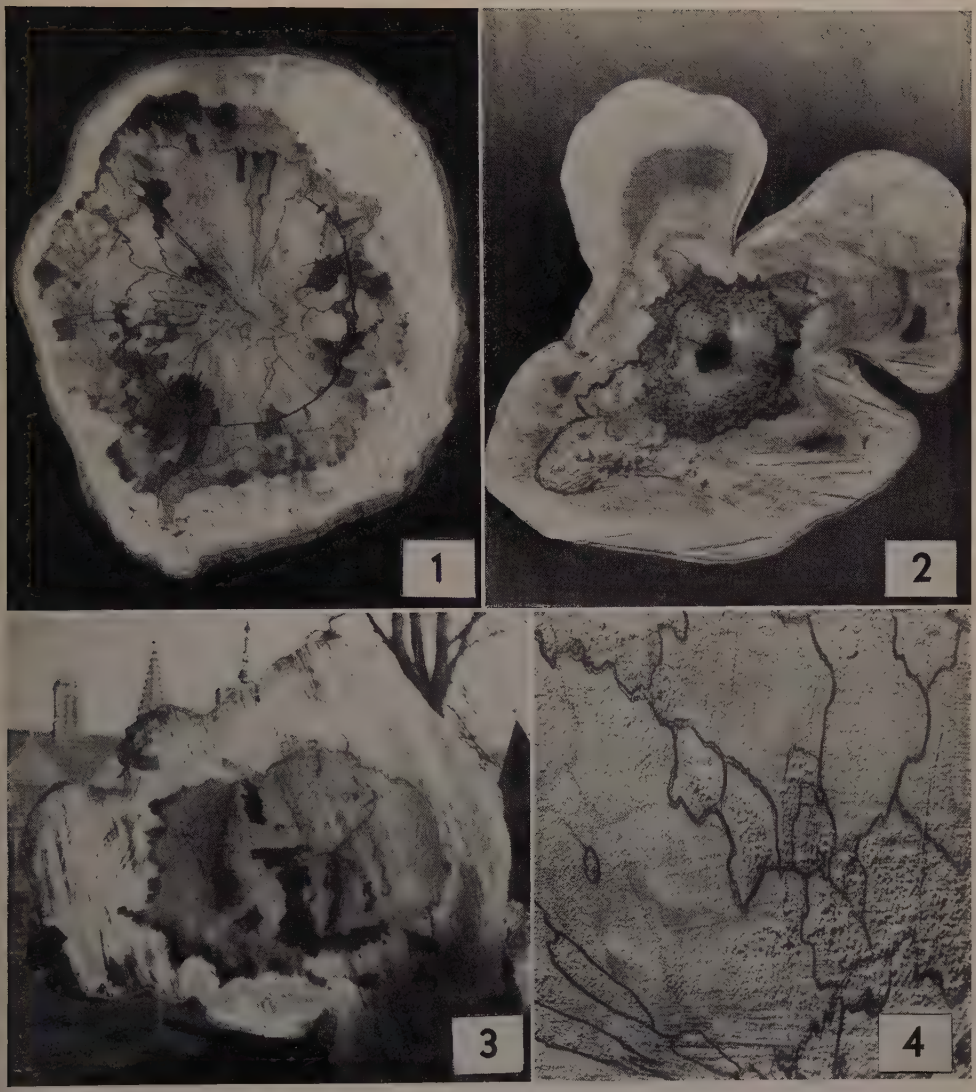
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INTERNATIONAL ASSOCIATION OF MICROBIOLOGISTS NOMENCLATURE COMMITTEE

Appointment of Judicial Commission on Bacteriological Nomenclature

At the Third International Congress for Microbiology held in New York City in September 1939, a series of recommendations of the Permanent International Committee on Bacteriological Nomenclature were accepted at the Plenary Session of the Congress. The third and fourth recommendations were:

> That the Nomenclature Committee, as at present constituted, shall continue to function under the auspices of the International Association of Microbiologists as it did under the International Society for Microbiology.*

> That the International Committee shall select from its membership a Judicial Commission consisting of twelve members, exclusive of members *ex officio*, and shall designate a Chairman from the membership of the Commission. The two Permanent Secretaries of the International Committee on Bacteriological Nomenclature shall be members *ex officio* of the Judicial Commission. The Commissioners shall serve in three classes of four commissioners each for nine years, so that one class of four commissioners shall retire at every International Congress. In case of the resignation or death of any commissioner, his place shall be filled for the unexpired term by the International Committee at its next meeting.

By prompt action at and subsequent to the Congress ballots were cast in spite of war conditions by 26 of the 62 members of the Permanent Committee on Nomenclature. These ballots when examined by the undersigned Joint Secretaries of the Permanent Committee in November 1942 were found to have resulted in the election of the persons whose names appear below. These are grouped in the three classes specified by the Permanent Committee, those receiving the highest number of votes being placed in the nine-year class, those receiving the next highest in the six-year class, etc. Names in the classes are arranged alphabetically.

Elected for nine years (term normally expires in 1948): R. E. Buchanan (U.S.A.), A. J. Kluyver (The Netherlands), E. G. D. Murray (Canada), S. Orla Jensen (Denmark). *Elected for six years* (term normally expires in 1945): J. Howard Brown (U.S.A.), A. R. Prévot (France), J. Ramsbottom (Great Britain), Th. Thjötta (Norway). *Elected for three years* (term normally expired in 1942): A. Lwoff (France), E. Renaux (Belgium), A. Sordelli (Argentine), C. Stapp (Germany).

It has been decided to make this arrangement in the hope that some plan for taking tentative action on questions of nomenclature can be developed by those members of the Commission who can be reached under war conditions.

While no provision was made in 1939 for the contingencies that have arisen, it is felt that those elected should serve until successors are elected. Prof. R. E. Buchanan has been asked to act as Chairman *pro tem.* of the Judicial Commission, as there is no possibility of securing an election under the rules as adopted.

ROBERT S. BREED (*Geneva, New York*)
R. ST JOHN-BROOKS (*London*)
Joint Permanent Secretaries, International Committee on Bacteriological Nomenclature

* The International Society for Microbiology was replaced in 1936 by the International Association of Microbiologists, which was formed by plenary resolution at the Second International Congress for Microbiology, London, 1936.

Note by Dr R. St John-Brooks, Lister Institute, Elstree, Herts

The functions of the Judicial Commission were defined by recommendations which were adopted by the Third International Congress for Microbiology, New York, 1939, in Plenary Session (see *Report of Proceedings*, p. 35). Any questions respecting interpretation of rules or recommendations in nomenclature may be submitted in the prescribed manner to the Chairman, but bacteriologists in Great Britain and the British Empire may find it convenient to refer their problems in this field in the first instance to Dr St John-Brooks, who will then take further necessary action.

It is hoped that the Judicial Commission will, among other matters, now be in a position to consider the proposed Bacteriological Code of Nomenclature which, under the aegis of the Nomenclature Committee, has been further developed by Prof. Buchanan and his collaborators since the last Congress for final disposition at the Fourth International Congress for Microbiology, whenever that may take place.

(*Accepted for publication* 14 *March* 1943)

THE MEASUREMENT OF PLANT DISEASES IN THE FIELD

In 1941 the Society's Plant Pathology Committee began an attempt to evolve practical and reliable standard methods of recording disease quantitatively in the field, and a first progress report on the scheme has already been published (*Trans. Brit. Myc. Soc.* XXVI, 1943, 28). Further experience was gained in 1942, when about 800 estimates of disease were received. The diseases concerned were potato Blight, potato-virus diseases, sugar-beet Virus Yellows, Take-all, Eyespot and Loose Smut of wheat, and apple Scab.

Various methods of estimating the extent of virus disease in potato and sugar-beet crops and of fungus diseases in cereal crops have now been adequately tested, and the Committee is satisfied that the following methods for use in survey and other work with these crops can be recommended as reliable and essentially practical. The method suggested for virus diseases of potato and sugar beet should be capable of application to most diseases of this nature. Further work is necessary before standard methods of measuring potato Blight and apple Scab can be recommended.

Virus diseases of potato and sugar beet. Where 1 % of disease or less is present in a crop it is usually sufficient to estimate the amount by visual examination according to Table 1.

Table 1

% of disease	Potato	Sugar beet
0	Not seen on field	Not seen on field
0–0·1	1 affected plant in 12 yd. radius	1 affected plant in 7 yd. radius
0·1–1·0	1 affected plant in 4 yd. radius	1 affected plant in 2 yd. radius

If more than 1 % is estimated in this way counts should be made by taking *random* samples on each of two diagonal traverses of the field. The number of plants to be counted depends on the accuracy needed. For general survey purposes five random samples of from 50 to 100 plants each would be adequate, whereas for special purposes, such as certification of crops, at least twice this number of samples would be desirable. The actual method of counting can be left to the individual observer, so long as it is done consistently from the random sampling position.

Cereal crops. Cereal Smuts, and Take-all (*Ophiobolus graminis* Sacc.), Eyespot (*Cercosporella herpotrichoides* Fron) and Brown Foot Rot (*Fusarium* spp.) of cereals as far as they have caused Whiteheads, can all be recorded from the same traverses of the field. Low percentages of disease can be estimated visually according to Table 2.

Table 2

% of disease	Limits
0–0·01	Less than 1 affected head in 50 sq. yd.
0·01–1·0	Less than 2 affected heads in 1 sq. yd.
Above 1·0	More than 2 affected heads in 1 sq. yd.

If more than 1 % is estimated, counts should be made by taking ten grab samples *at random* on a zigzag or diagonal traverse of the crop. Each sample should contain not less than 20 eared tillers. To ensure random sampling a grab may be made with both hands extended and eyes closed. The stem bases of the 200 or more eared tillers thus collected which shew Whiteheads should be examined and separated into three groups according as they are attacked by *Ophiobolus*, *Cercosporella* or *Fusarium*. The percentage number of tillers substantially attacked by the different organisms can then be calculated. The amount of Smut present can be determined from the numbers of ears affected. Smut may also be estimated by counts of suitable samples when the crops are in stook.

(*Accepted for publication* 4 *April* 1943)

PROCEEDINGS

Meeting held in the rooms of the Linnean Society of London, 13 February 1943.

The President, Dr S. P. Wiltshire, M.A., in the Chair.

N. C. Preston. Some observations on the genus *Myrothecium*.

Professor A. Fleming and G. Smith. Some methods of mounting and preserving mould cultures.

H. A. Dade. Application and uses of Fleming's mounting methods.

Miss B. J. Legge. On *Phytophthora* crown rot of *Campanula* with reference to soil-borne infection.

S. Dickinson. Experiments on the physiology of obligate parasitism. 4. The growth of rust mycelium from out of infected leaves.

C. T. Ingold. Two aquatic Hyphomycetes.

Meeting held in the rooms of the Linnean Society of London, 16 April 1943.

The President, Dr S. P. Wiltshire, M.A., in the Chair.

Reports from the Society's Committees

Plant Pathology Committee. Secretary: J. H. Western.

G. R. Bisby. The list of common British plant diseases.

W. Buddin. Plant disease measurement.

Nomenclature Committee. Secretary: Miss E. M. Wakefield.

Edible Fungi Sub-Committee. Convenor: J. Ramsbottom.

Foray Committee. Secretary: Mrs E. W. Mason.

REVIEWS

Aquatic Phycomycetes exclusive of the Saprolegniaceae and Pythium. By FREDERICK K. SPARROW Jr. Pp. xix + 785, frontispiece and 69 text-figures. (University of Michigan Studies, Scientific Series, 15.) University of Michigan Press and Oxford University Press, 1943. $5.

Dr Sparrow's *Aquatic Phycomycetes* will have a warm welcome from the members of the British Mycological Society, many of whom know the author. Those who were at the Haslemere Foray in 1932 (*Trans. Brit. Myc. Soc.* XVIII, 1933, 7) will recall the surprising collection of aquatic fungi that Dr Sparrow made from the small pond behind the Haslemere Educational Museum, and more will remember the talks he gave at our meetings.

The scope of the book has been limited deliberately to those Phycomycetes which live in water, except for those specially mentioned in the title. Some genera of lower fungi, such as *Synchytrium* and *Physoderma*, are omitted; and some groups, notably the Plasmodiophorales, are described only in part. The omissions are not disadvantageous, for the adoption of a biological criterion to fix the limits of the book has enabled the author to obtain a unity which could hardly have been got in any other way.

Within the boundaries he has set, Dr Sparrow presents an enormous mass of detail, impossible to analyse in a short review. Much of this detail is drawn from his own observations, for he has travelled widely in Europe and America, and has seen in the living state very many of the fungi he describes. To his great practical experience of the organisms he has joined a thorough and critical study of the work of his forerunners. This union gives to us a masterly and comprehensive account of the Phycomycetes found in water, and the account may be regarded as practically complete to the date of publication of the book.

No doubt because he has worked and thought so much, Dr Sparrow takes up a conservative position. He knows well that there remain many gaps in our knowledge and that those gaps can be filled only by more observations. He does not hide his own views, but he states them without dogmatism; there is a very pleasant absence from the book of pontification and of special pleading designed to support some pet theory. The author is clearly much more interested in his subject than he is in himself, and he very successfully preserves the objective attitude so desirable in botanical writings.

All students of aquatic life, whatever their special interests, will find *Aquatic Phycomycetes* of very great help. The book sets out plainly what is known, and describes methods by the use of which more may be learned. We may well hope that when the present troubles are over, Dr Sparrow's book will promote an intensive investigation of aquatic fungi, for now those who desire to study those organisms have a reliable guide to point the way.

The University of Michigan is to be congratulated on the addition of another valuable book to their scientific publications. If the reviewer may be allowed one grumble, it might have been better if so large a book had been issued in two volumes. B. BARNES

A Dictionary of the Fungi. By G. C. AINSWORTH and G. R. BISBY. Pp. viii + 359, 138 figs. Imperial Mycological Institute, Kew, 1943. 20*s*.

A dictionary of the fungi in English and of convenient size has long been desirable. Drs Ainsworth and Bisby have now produced a useful and welcome volume which is considered to include a list of generic names of the fungi complete to the end of 1939; supplementary material has already been printed in the *Review of Applied Mycology*.

The book is an alphabetic arrangement of the names of genera and groups of higher rank, with the names of the more important plant diseases, many technical terms, some sixty-four longer sections dealing briefly with most of the general matters that interest mycologists, and ten short biographical notices of outstanding mycologists of the past. The lichens are described in a general section, but the genera are not listed; a few bacterial genera are listed. Prof. G. W. Martin has allowed his well-known scheme of classification to be printed as an appendix. The illustrations are grouped at the end, where they are easily found.

The more a reader browses in the book the more it becomes clear that it is a useful tool. The numerous references to original sources show where additional information may be sought, so that the dictionary is a guide to the books as well as to the fungi. The working mycologist cannot be without this dictionary, and the undergraduate will find it of service to him. No doubt, the specialist will find fault here and there. Perhaps he will send on his comments to the authors, for this Dictionary should go into subsequent editions, and necessary changes can then be made. The book deserves well of British mycologists.

B. BARNES

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